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DEMOGRAPHY, BEHAVIOR, AND PROTEIN POLYMORPHISM IN SUBARCTIC *CLETHRIONOMYS GAPPERI*

by

©

STEVE MIHOK

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
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THE UNIVERSITY OF ALBERTA
FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled

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SUBARCTIC *CLETHRIONOMYS GAPPERI*

submitted by STEVE MIHOK

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ABSTRACT

Chitty's (1967) hypothesis was examined as a mechanism for population regulation in subarctic red-backed voles (*Clethrionomys gapperi*) near Great Slave Lake, Northwest Territories, Canada. Demography, behavior, and genetics were studied during a peak (1976) and a decline (1977).

Multiple capture trapping on a 6.25-ha grid from spring to fall revealed that the peak was primarily the result of good juvenile survival. The decline was related to poor overwintering survival of all age-classes and poor juvenile survival. Spring breeding densities from 1976 to 1978 were relatively constant. Numbers of mature females throughout the season were also relatively constant, and resulted in similar reproductive outputs in both years. Mature females were territorial. Mature males lived in large, extensively overlapping home ranges. Immatures settled into small, moderately exclusive ranges in vacant areas. Multiple captures accounted for about 23% of all captures, with immatures involved in more multiple captures than matures. Multiple captures increased with density as a consequence of increased spatial overlap between animals. Social structure was loosely organized around an animal and its neighbors. There were no major differences in spatial patterns or social structure between years.

Young born to wild-caught females were raised in outdoor pens during the decline. Growth was affected by day of birth, litter size, sex, condition of the mother, and transferrin phenotype. Maturation followed typical seasonal trends, with a two-week transitional period occurring at about the time of the summer solstice. An ageing technique based on M^2 tooth measurements was developed.

Counts of wounds on animals captured in the general area showed that immatures had few wounds, as did all animals during the decline. Wounding was highest in matures during 1976, peaking in mid-summer when young, mature individuals were recruiting into the population. Year differences in wounding were related to the number of animals contacted rather than differences in levels of aggression.

Animals from the general area were paired in a series of neutral arena tests. The behavioral repertoire of C. *gapperi* is described. Factor analyses of 22 behavioral variables revealed four repeatable factors representing amicable, threat, attack and subordinate behavior. Analyses of dominance indicated a linear hierarchy consisting from top to bottom of overwintered females, young mature females, immature males, immature females, overwintered males, and young mature males. Behavioral differences were related to sex, age, and maturity, and were not related to year differences. Multivariate discriminant analysis of winners and losers indicated that they were caught in different habitats.

Polyacrylamide gel electrophoresis of transferrin

revealed changes in allele frequency that were correlated with changes in density. Selection favored the heterozygote in early-summer and one of the homozygotes in winter. Fitness at the transferrin locus could not be related to behavior.

Chitty's hypothesis was not tenable for *C. gapperi* in terms of behavior, but was correct in predicting qualitative changes in the population. *C. gapperi* reproduces at a maximal rate under subarctic conditions, and may never reach breeding densities sufficient for self-regulation of density (Andrewartha and Birch 1954).

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TABLE OF ABBREVIATIONS

OW	Overwintered
YG	Young of the year
Y+	Young mature
Y-	Young immature
M	Male
F	Female
DF	Degrees of freedom
N	Sample size
P	Probability
r^2	Coefficient of determination
X^2	Chi-square statistic
Tf	Transferrin
FF	Fast-Fast Homozygote
SF	Slow-Fast Heterozygote
SS	Slow-Slow Homozygote
Att	Attack
Avo	Avoid
Cha	Chase
Fgt	Fight
Fol	Follow
Got	Groom other
Grm	Groom self
Hes	Hesitant approach
Hud	Huddle
Na	Nasoanal
Neu	Neutral approach
Nn	Nasonasal
Paw	Pawbeat
Pw1	Pawbeat 1
Rai	Raise
Rap	Raise partially
Ret	Retreat
Str	Stretch approach
Sub	Submissive
Tur	Turn away
Voc	Vocalization
Wit	Withdrawal
AGG	Attack factor III
AMI	Amicable factor I
APV	Approach-avoidance factor VII
AVD	Avoidance factor V
BOX	Boxing factor VI
SBT	Subordinate factor IV
THR	Threat factor II

INTRODUCTION

Population densities of small mammals in boreal regions fluctuate in an annual cycle related to relatively predictable changes in reproduction and recruitment in a seasonal environment. In microtine rodents, a superannual cycle in density with a periodicity of two to five years is often superimposed on this annual cycle (Krebs and Myers 1974). This superannual cycle is thought to be a common feature of the demography of all microtines, and has been the focus of intensive research for about 40 years. Researchers have searched for consistent patterns in the demography of different species, and have identified a general syndrome of events associated with superannual fluctuations in density (Krebs and Myers 1974). In the search for a unifying theory to explain this syndrome of events, various hypotheses have been advanced, including : food (Cole and Batzli 1978), weather (Fuller 1977a), stress (Christian 1978), predation (Andersson and Erlinge 1977), behavior (Krebs *et al*. 1978), genetics (Chitty 1967), dispersal (Tamarin 1978), and a multi-factor model (Lidicker 1978). One of these hypotheses, the *polymorphic behavior* hypothesis proposed by Chitty (1967), was chosen as the starting point for this study.

Working Hypothesis

Chitty (1967) proposed that behavioral interactions are responsible for the regulation of population density in any species, whether it is cyclic or not. In brief he proposed the following:

(1) Temporal variation in aggressive behavior exists in a population, such that "aggressive" behavior is common at high density and "nonaggressive" behavior is common at low density.

(2) This behavioral variation is due to changes in the "quality" of the population. Qualitative changes result from a high proportion of aggressive "types" at high density, and a high proportion of nonaggressive "types" at low density.

(3) Behavioral types are genotypes rather than just phenotypes, i.e. aggressive behavior is a quality of the individual rather than the situation and is heritable.

(4) Aggressive types are at a selective advantage relative to survival, but are at a selective disadvantage relative to reproduction. Therefore the net fitness of each type varies as a function of the degree of mutual interference between animals, which is presumably a function of population density.

Given these four assumptions, population changes take place as follows:

(1) At low density, mutual interference is low since resources (e.g. space) are abundant. Aggressive types therefore have only a minor selective advantage over nonaggressive types in survival. This is counterbalanced by a much higher selective advantage in reproduction in the nonaggressive type. Consequently, nonaggressive types form the main part of the population.

(2) As density increases, mutual interference becomes a significant factor in determining the fitness of animals as they presumably compete for resources. The aggressive type competes better and therefore survives better, even though it does not reproduce as well as the nonaggressive type. Consequently, the aggressive type gradually replaces the nonaggressive type in the population.

(3) At high density, mutual interference is high, the population is mainly composed of aggressive types, and the net reproductive output of the population is consequently very low. This precipitates a decline in numbers.

(4) As density decreases, mutual interference loses its importance in determining the survival, and hence fitness of the different types. The nonaggressive type is therefore selected for because of its higher reproductive output. Nonaggressive types gradually replace the aggressive types in the population and the cycle repeats itself.

Testability

Krebs (1978) has reviewed some of the implications of Chitty's hypothesis, and has listed 13 predictions that arise from it. Although some of these predictions are testable through experimentation, the underlying assumptions of Chitty's hypothesis and its mechanism of action are not easily testable. In particular, the behavioral type, the cornerstone of the hypothesis, has not been identified in any population to date, and may never be found with current methods of assessing behavior (Mihok 1976). This is mainly due to our poor understanding of the behavior of microtines (Krebs 1970; Turner and Iverson 1973; Conley 1976; Mihok 1976). In contrast, our understanding of genetic changes in cyclic populations is growing, as genetic changes have now been documented in many species and localities (Gaines *et al.* 1978).

In this study, I have attempted to define the possible mechanisms of action of Chitty's hypothesis in precise ecological and utilitarian terms. In particular, I have attempted to monitor demography, behavior and genetics during sharply contrasting years of population growth, when events described by Chitty (1967) should be easily observed and quantified.

Study Area and Animal

Studies were conducted in the vicinity of the Heart Lake Biological Station, just south of Great Slave Lake, Northwest Territories, Canada. The area is located within the boreal forest in a zone of discontinuous permafrost at the boundary between the Alberta Plateau and the Mackenzie Lowlands (Fuller 1969). A limestone escarpment separates the two regions and supports most of the upland forest near the Biological Station. Well-drained habitats dominated by white spruce (*Picea glauca*), jack pine (*Pinus banksiana*), and aspen poplar (*Populus tremuloides*) are patchily distributed along the escarpment, and are surrounded by extensive black spruce (*Picea mariana*) and tamarack (*Larix laricina*) bogs or wet sedge meadows. The climate is continental, with a long, cold and dry winter, and a short, warm summer. Snow covers the ground from early November to late April and can reach depths up to about 100 cm (Fuller *et al*. 1969).

The study animal, a microtine rodent, the red-backed vole (*Clethrionomys gapperi athabascae*), is within 40 km of its northern range limits at Heart Lake (Banfield 1974). It is active throughout the year (Stebbins 1972; Herman 1977), but only breeds during the summer months (Fuller 1969, 1977a). Population densities are considerably lower than those observed in southern populations (Fuller 1977a; Miller and Getz 1977; Merritt and Merritt 1978a), and home ranges are considerably larger (Beer 1961; Iverson and Turner 1972; Wells 1976; Merritt and Merritt 1978b). The species is mainly granivorous at Heart Lake, but feeds on considerable amounts of green vegetation in spring, fungi in summer, and lichens and other vegetation in winter (Dyke 1971). Among the smaller "mouse-like" mammals in the area, red-backed voles are generally the numerically dominant species in well-drained forest habitats. They are also present in smaller numbers in poorly-drained bog habitats, which are dominated by *Microtus pennsylvanicus* (Doyle 1979). The vole population at Heart Lake goes through a nearly complete turnover each year, and appears to be cycling in density with a periodicity of about four years (Fuller 1969, 1977a, unpublished).

Objectives

My overall objective was to quantify the spatial, behavioral and genetic changes that occur in contrasting years of population growth. The study mainly dealt with two years, 1976, a year of peak numbers possibly out of synchrony with the long-term population cycle at Heart Lake (Fuller 1969, 1977a), and 1977, a post-peak or early-decline year. The study involved four major sub-sections:

(1) a census of a field population to obtain demographic and spatial data,

(2) laboratory observations of behavior in animals sampled from the general area,

(3) monitoring of wounding in animals caught over a wide area by various researchers,

(4) electrophoretic studies aimed at detecting genetic changes.

Some of the general questions I attempted to answer were as follows:

(1) Is *Clethrionomys gapperi* a typical microtine, i.e. does it conform to the syndrome of events described in Krebs and Myers (1974)?

(2) At what times, and in what segments of the population, do forces limiting population growth act?

(3) Do qualitative (i.e. genetic) changes occur in the population with time, and are these associated with the population cycle?

(4) Are there changes in the type, pattern or frequency

of behavioral and spatial contacts associated with the population cycle?

(5) Are behavioral patterns related to components of fitness such as dominance status, home range size, survival, reproduction, occupation of optimal habitat, etc?

(6) Are different methods of analyzing behavior (neutral arena trials, spatial analyses, wounding indices) useful in monitoring behavioral changes; do they measure the same thing?

METHODS

Multiple Capture Grid

Exploratory trapping was done on an 18-ha plot (Wells 1976) near the Heart Lake Biological Station from June to August 1975. This led to selection of a 6.25-ha area, with a high density of small mammals, for intensive sampling in 1976 and 1977 (Grid A, Fig. 1). An 11 X 11 grid of 121 traps at 25-m spacing was sampled at two-week intervals, from May to September of each year with some exceptions (Table 1), caused by interference by black bears (Ursus americanus) and logistic problems. An additional sample was obtained in early May of 1978. The grid was subsequently live-trapped from May to August (J. Douglas May, pers. comm.), and was intensively snap-trapped in late-September (Steven S. Beare, pers. comm.). In each sampling period (rota), traps were opened on the night of day 0, checked in the morning and evening of days 1 to 4, and closed following the ninth check on the morning of day 5.

Each animal was toe-clipped on first capture and weighed with a Pesola spring balance at least once in each rota. Reproductive condition was generally noted on each capture (males: testes scrotal or abdominal; females: vagina perforate or imperforate, nipples visible or not, pubic symphysis closed or parted). Any signs of wounding were noted.

The traps consisted of a wooden box (9 X 15 X 24 cm) with a built-in metal tunnel (4.3 X 4.3 X 5.7 cm). Access to the tunnel was limited by a 2.5 cm diameter hole cut into the front of the trap. The tunnel contained a sloping plexiglass door which permitted entrance into the trap but prevented exit. Two holes cut into the sides of the trap were covered with wire mesh to allow an approaching animal to detect the presence of animals already captured. Terylene fibre was provided for insulation, and sunflower seeds were replenished as required for food. Traps were never cleaned beyond minimal scraping (Boonstra and Krebs 1976), and were left in place, closed and unbaited, between sampling periods.

Animals were classified as mature or immature, overwintered or young of the year. Males were considered to be mature if they were scrotal at any time. Females were considered to be mature if the vagina was perforate, nipples were visible, or the pubic symphysis was parted at any time. All other animals were considered to be immature. Ages were assigned on the basis cf body weight from general trends for the Heart Lake area (Fuller 1969, 1977a, 1977b). Overwintered voles of known age typically weighed about 24 g in early July, when the first young were caught at about 15 g. From late July on, voles could not be accurately separated into age-classes, and all newly-caught mature individuals were considered to be young of the year.

General Trapping

Animals were live-trapped for behavioral experiments from 2 May to 6 October 1976, and from 29 April to 6 October

1977. Traps were set in a standard fashion each week (with a few exceptions) within about 15 km of the Biological Station and were run for four days. A given area was rarely sampled more than once each year. A standard set consisted of four lines of 28 Sherman traps (23 X 9 X 8 cm) each, spaced at 10 m intervals, with two lines on each side of the Mackenzie Highway, spaced 50 m apart. Peanut butter was spread on the treadle of the trap for bait, and a small plastic bag of sunflower seeds was suspended from the rear door for food. Trapping deviated from the normal pattern only in the fall of 1977, when most of the animals used in behavioral experiments were obtained from traplines run by other people (D. H. May, S. Pickering). Animals were also trapped from June to August 1975 and in early July 1978. Methods were not standardized in those years and Longworth traps were occasionally used. Animals captured were used in behavioral experiments in 1975 (Mihok 1976), or were a source of blood samples for electrophoresis in 1975 and 1978.

All Clethrionomys gapperi were taken to the laboratory where their sex, weight, and external reproductive condition were noted. All but the youngest of voles were given a fingerling ear tag with an attached, coloured plastic disc for identification. Animals were then individually maintained in opaque plastic cages (16.5 X 25.5 X 48.5 cm) containing abundant commercial rodent chow, water, terylene bedding, and wood shavings, and were housed in a garage that was open to environmental conditions. Each vole was given a minimum of one day in captivity before any behavioral tests were conducted, to allow recovery from the stress of capture, and permit some degree of acclimation to captivity.

Neutral Arena Tests

Behavioral observations were conducted in a hexagonal arena 60 cm in diameter and 47 cm high. The arena was subdivided by a central partition that could be raised by means of a rope and pulley. Two 40-W red bulbs placed 50 cm from the floor provided illumination. The floor was covered with 2-3 cm of wood shavings that were changed after a maximum of six trials. The arena was occasionally washed to minimize olfactory cues left from previous trials. I observed voles from within a darkened blind through a 31 X 20 cm pane of semiopaque glass in one wall of the arena. The test area was a screened porch and was subject to environmental light and temperature. Experiments were conducted between 2100 and 0200 hours, the normal summer activity peak of *Clethrionomys gapperi* (Stebbins 1972).

A behavioral trial consisted of a standard procedure in which two voles were sequentially placed in opposite halves of the arena. They were given 2 min to investigate their half of the arena, after which the partition was raised. For the next 15 min I recorded the occurrence of various behaviors for each vole with the aid of a keyboard-activated Esterline Angus 20-channel event recorder. A verbal description of the trial was also recorded on cassette tape when rare behaviors occurred.

Four males and four females were randomly selected for each set of behavioral observations as they became available from trapping. On day 1 a round-robin sequence of six within-sex trials was conducted for each sex (A vs B, C vs D, A vs D, B vs C, A vs C, B vs D). On day 2 four between-sex trials were conducted (A vs a, B vs b, C vs c, D vs d). Each vole therefore participated in three within-sex trials and one between-sex trial. Voles were transported to and from the animal house in light-tight containers (15 X 15 X 10 cm), and were also held in these containers between trials on day 1.

Autopsy

Males were killed and autopsied on day 3 of behavioral observations, but females were held until it was clear that they were not pregnant. At autopsy, voles were weighed and measured using standard methods (Fuller 1977b). Reproductive organs were examined to determine reproductive status. Skins were everted and the moult pattern was described verbally or with the aid of a diagram. The number of wounds visible on the everted skin was recorded. Recent wounds resulting from attacks in the arena were easily identified and were not recorded. Wounds were classified as being either light or severe. Light wounds appeared as paired pigmented scars, and were probably older wounds that had healed. Severe wounds appeared as paired punctures in the skin and were probably recent bites that had not healed. Since the exact correspondence of these marks to actual wounding was not determined (Rose and Hueston 1978), the terms "light" and "severe" are used to avoid bias.

Skulls were saved for later classification into age groups based on development of roots on the second upper molar (M^2, Tupikova *et al*. 1968). Young of the year were classified into three categories: anterior labial groove open, groove closed, and roots formed. Overwintered animals were identified with 100% accuracy in that they all had root lengths much longer than those of young of the year. In the rooted category, the distance from the tip of the anterior root to the saddle between both roots was used as an index of root length. In the closed groove category, the distance from the edge of the closed part of the groove to the basal end of the tooth was used as an index of groove closure. Tooth length was measured in all categories along the anterior labial surface. Measurements were made with a calibrated ocular micrometer and were recorded to the nearest tenth of a millimeter.

Captive Voles

All females were observed daily for signs of parturition. Females about to give birth were transferred to a large cage (30 X 48 X 20 cm), and checked two to three times a day. Nestlings were counted on the day of birth.

In 1976, most pregnant females were killed in the second week after parturition, but seven litters were maintained until weaned on day 21, when the young were weighed, sexed, toe-clipped, and assigned to mixed-sex, mixed-litter pairs in small cages. On 14 July the litters were transferred to six large pens (2.4 m X 2.4 m) located in a natural clearing at the Biological Station (Friesen 1972). The pens were provided with nest boxes of various sizes, feeders filled with rodent chow, and water bottles. A considerable amount of debris (branches, logs, rocks) was also placed in each pen. Each pen was set up with three of the original pairs from different litters. The pens were periodically checked for litters and deaths until 23 August when all individuals were removed and killed.

In 1977, members of all 46 litters born in captivity were maintained until day 21 when they were transferred to the pens. An approximate 1:1 sex ratio was maintained in each pen, and littermates were separated as far as possible. Littermates were removed and killed as they reached about 50 days of age. This kept the number of animals per pen at about 5 in early July, 10 in late July, and 15 in August. On 21 August the remaining animals were killed to obtain animals at various ages. The pens were then used for raising late-summer litters, with densities reaching a maximum of 10 voles per pen by mid-September. On 24 September all remaining voles were killed.

Behavioral Grid

In 1977 a second live-trapping plot was set up about 775 m from the multiple capture grid (Grid B, Fig. 1). A 10 X 10 grid of 100 Sherman traps at 25-m spacing was run by methods similar to those used on the multiple capture grid.

Traps were operated between each session of multiple capture trapping, beginning on 15 May and ending on 25 August. The rota scheduled for 29 May was skipped so that traps could be repaired after a bear damaged them.

Voles captured on this grid were temporarily removed on the morning trap check for behavioral tests in the neutral arena. They were returned to the field after about a 2-3 hr absence. A maximum of two males and two females were removed each morning. During the last rota (25-29 August), all voles were brought to the lab, killed, and autopsied.

Standard Behavioral Opponents

In 1977 I observed the behavior of "standard voles" and animals temporarily removed from the behavioral grid in the neutral arena. Before females came into estrus in May, eight females and eight males were captured and run through the usual sequence of neutral arena tests. Instead of being killed, these voles were saved for use as standard opponents. They were kept in the normal animal house, but were maintained in large cages (30 X 48 X 20 cm) with activity wheels. Four animals of each sex were selected as standard opponents in May. Deaths of two females in June and one male in early July resulted in three replacements to the original set of animals. Only four trials were staged between field opponents and the original three voles that were replaced. Standard voles were run through the normal within-sex, round-robin sequence of behavioral trials during the first week of each month until September to monitor behavioral changes.

Within-sex behavioral trials were conducted between standard voles and field opponents in the usual manner in the neutral arena with two differences. Animals were only allowed a 1 min acclimation period, and the observation period was shortened to 10 min. Individuals were removed from the field on two mornings, and were paired with two standard opponents each morning (for a total of four trials, with a different opponent for each trial). Standard voles only participated in one trial each morning.

Photography

In 1977 additional behavioral observations were conducted in a larger arena (87 X 55 cm) on day 3 before animals used in netural arena trials were autopsied. Up to eight animals in various combinations were observed between 1000 and 1400 hours for about an hour during each session. Behavior was not quantified as in the neutral arena tests. Instead, twenty to forty photographs of interactions were taken. Five of these sessions were specifically set up with four mature males and one potentially estrus female (one day post-partum). One session included nestlings and one included 19-day old littermates. Three sessions were run with other species (*Peromyscus maniculatus*, *Microtus pennsylvanicus*, *Phenacomys intermedius*) present.

Electrophoresis

Blood samples were obtained from all animals captured in general trapping by inserting a pipette into the suborbital sinus of the right eye prior to autopsy. Serum was separated out by centrifugation (5000 g for 2 min) and stored in a chest freezer at about -6°C at the Biological Station. Samples were transported to the University in the fall where they were stored in a freezer at about -20°C. Samples were processed between October and December of each year.

Various techniques of disc gel electrophoresis were used in 1975 to assess the degree of protein polymorphism in vole serum. After a single overview of all samples using Coomassie Blue as a general protein stain, I concentrated my efforts on only one protein, transferrin. Transferrin produced clear bands on polyacrylamide gel and I felt that it could be reliably typed with some refinement of technique. The methods adopted were those originally reported by Davis (1964). A 7.5 microliter sample of serum was first mixed with an equal amount of 40% sucrose that contained 0.1 g/l of ferric ammonium sulphate. Samples of this mixture were then electrophoresed through a small pore gel for about 1.3 hr at 260 V and 300 Hz in an Ortec model 4100 apparatus modified to hold tubes rather than slabs. At the end of the run, gels were cut at the migration point of bromphenol blue for standardization between tubes, and were stained with Nitroso R salt solution (Smith 1968) to bring out the transferrin bands.

Habitat Surveys

Each trap station where an animal was captured during general trapping was scored for a number of habitat features (Table 2). Each trap station on the multiple capture grid was also scored for habitat features in early-August 1977. Tree and shrub species within about 5 m of the trap site were scored on an eight point scale according to percentage cover. Graminoids and sedges, mosses, and lichens were lumped into three general categories, and were also scored on an eight point scale. Other plants within about 2 m of the trap site were scored on a six point scale. Estimates of microrelief (fallen logs, rocks, crevices) and ground moisture were also made on an eight point scale.

Additional Sources of Data

Continuous snap-trapping of the forest in the vicinity of the Biological Station by W. A. Fuller and his party provided additional data augmenting sample sizes for analyses of demography and wounding. Methods are outlined in Fuller (1977a). Transferrin data from Canham (1969) and McPhee (1977) were included in some electrophoretic analyses. Canham (1969) erroneously classified all mature individuals as overwintered. His data from 1966 and 1967 were reclassified on the basis of M^2 root lengths. Data for 1975 were combined with the data of McPhee (1977), after correcting a few of his transferrin typings on the basis of his reported migration rates.

Computer Analysis

The SPSS package of programs (Nie et al. 1975) was used for most statistical tests. Cluster analyses were done with the programs in Clustan 1C (Wishart 1975). Other analyses, not covered by these packages, were performed with programs written by myself in Pl/C or Pl/1. Three-dimensional stick diagrams were produced by the program PHYSETER (R. A. Gibson, University of Toronto).

RESULTS

Demography

Small Mammal Community

Red-backed voles and deer mice (*Peromyscus maniculatus*) were the only small mammals regularly captured on the multiple capture grid. In total, 273 red-backed voles and 193 deer mice were captured 4638 times from 1976 to 1978. One least chipmunk (*Eutamius minimus*), one ermine (*Mustela erminea*), one arctic shrew (*Sorex arcticus*), and three heather voles (*Phenacomys intermedius*) were also captured. In 1977, 15 masked shrews (*Sorex cinereus*) were caught when young shrews from high density lowland populations dispersed into upland habitats (Doyle 1979). Numerous red squirrels (*Tamiasciurus hudsonicus*), and the occasional pine marten (*Martes americana*) were also seen on the grid.

Numbers

As an index of population density, I calculated the minimum number of animals known to be alive in each rota. The number of animals not enumerated when known to be alive averaged 4.4% (19 of 433). This high level of efficiency indicated that the index was a reliable estimate of numbers in the "trappable" population (Hilborn *et al*. 1976). Young animals (Boonstra and Krebs 1978), and subordinate animals (Watts 1970a), are rarely caught in live traps, and I therefore have no direct estimate of "true" population size. Spring numbers were relatively constant from 1976 to 1978, but fall numbers differed dramatically (Fig. 2). Numbers can be crudely converted into densities by dividing by an area that takes into account animals whose home ranges partially overlap the grid (calculated by adding a boundary strip equal to 1/2 the mean Adjusted Range Length (Stickel 1954) of animals caught more than five times, Appendix 1).

In 1976, the population reached a fall density of about 8.2 animals/hectare, which is comparable to a previous peak recorded in 1974 (Fuller 1977a). These peak populations of 1974 and 1976 represent the highest densities recorded at Heart Lake since studies began in the early 1960's (Fuller 1969). In 1977, the population failed to increase beyond typically low to average densities for the Heart Lake area, reaching a final density of about 2.2 animals/hectare. Taking into account the variable area sampled by the grid (Appendix 1), numbers reflect an eight-fold increase in density from spring to fall in 1976, and a three-fold increase in 1977.

Peak numbers in 1976 appeared to be a general feature of the population dynamics of the three abundant cricetids in the Heart Lake area. Numbers of *Peromyscus maniculatus* caught on the multiple capture grid in 1976 were high (Mihok 1979), as were numbers of *Clethrionomys gapperi* and meadow voles (*Microtus pennsylvanicus*) caught on a removal grid in a black spruce (*Picea mariana*) fen about 1.5 km from the multiple capture grid (Doyle 1979).

Survival

Minimum 14-day survival or residency rates were calculated from the midpoint of each rota to the midpoint of the next rota:

$$\text{Survival} = e^{[\ln N(t+1) - \ln N(t)] \times 14/dt}$$

where $N(t)$= number known to be alive in rota t, $N(t+1)$= number known to be alive in the rota after rota t, and dt= interval between rotas in days. Periods of poor survival (<0.71, Krebs *et al.* 1969) occurred at various times in different age groups (Table 3). Due to small sample sizes, it was impossible to show that any of this variation in survival was statistically significant. Survival rates in all subcategories of the population were also compared by lumping data for each year. Overwintered females probably survived better in 1977, but other animals survived equally well in both years (Table 4). Note that these rates only measure survival after an animal has become part of the "trappable" population.

Winter survival rates calculated from the disappearance of marked voles from one fall to the next spring were relatively high when expressed as 14-day rates (1976-77: 0.86, 1977-78: 0.93), but still resulted in a considerable reduction in numbers (Fig. 2). Voles survived the winter of 1977-78 better (32% vs 9%) than the winter of 1976-77 (X^2=11.14, $P < 0.001$). Although survival rates varied, the absolute number of animals surviving through each winter was nearly identical. Eleven animals survived the winter of 1976-77, and ten animals survived the winter of 1977-78 (five unmarked animals were caught in rota 1 of 1978). Mature and immature voles, and males and females were equally likely to survive winter (20% vs 12%, $X^2=0.73$, $P > 0.25$; 12% vs 16%, $X^2=0.38$, $P > 0.5$).

Reproduction

Reproduction probably started about 10 days earlier in 1977 than in 1976 (Table 5), as dates of overwintered litters were marginally earlier (first litter: $t=2.17$, $P < 0.05$; second litter: $t=2.24$, $P < 0.05$). Data from births in captivity to wild-caught females were combined with extrapolated births from visibly pregnant snap-trapped females to increase sample sizes. The extrapolated date of birth was determined from embryo lengths using the guidelines reported by Ożdżeński and Mystokowska (1976) for bank voles (*Clethrionomys glareolus*).

Although dates of birth were determined accurately, it was impossible to correctly determine the parity of females due to disappearance of placental scars (Martin *et al*. 1976). Fourteen females were caught with large, hairless nipples that had obviously been suckled, subsequently gave birth in captivity, and had only one set of placental scars at autopsy. These females should have had two sets of scars, one set representing the litter born in the field, and one set representing the litter born in captivity. The disappearance of placental scars probably accounts for the extreme range and variance in the estimates of the dates of litters. In particular, dates of second litters are probably exaggerated by the inclusion of some third litters in the second litter category. Dates must therefore be interpreted with caution, since there is no good estimate (10-20%?) for the error attributable to mistakes in the assignment of parity.

Pregnancy rates were determined by allowing females to litter in captivity. During the main part of the breeding season (May 18 to August 7), 80 of 85 females captured on Sherman traplines were pregnant. Only females weighing at least 18 g were included in this calculation, since immature females (imperforate vagina, threadlike uterus) occasionally weighed up to 18 g. The five females which were not pregnant had open pubic symphyses when captured, indicating that they were probably caught before post-partum estrus occurred. These data imply that pregnancy rates were very close to 100% during the main breeding season. Mature females (perforate vagina, thickened opaque uterus) that were not pregnant were only caught towards the beginning or the end of the breeding season, as there was considerable variation in the dates of first and last litters (Table 5). The gestation period of _Clethrionomys gapperi_ was estimated at 22 days (twice the mean number of days from capture to parturition). Two observed copulations resulted in litters 20 and 22 days later. These estimates of the gestation period are much lower than the interval between the mean dates of first and second litters in overwintered females (37 days, Table 5). Given nearly 100% pregnancy rates, the interval between mean dates of first and second litters should have been equal to the gestation period. This discrepancy presumably reflects mistakes in the assignment of parity due to the disappearance of placental scars. Delayed implantation and abortion may also account for this discrepancy, but I have no good evidence for these phenomena from field data. Overwintered females living on the multiple capture grid dropped litters at three to four week intervals, and were therefore capable of producing up to four litters in each breeding season, although few survived to do so (Table 3).

Litter sizes at birth were estimated from counts of young born to wild-caught females. A 3-way Analysis of Variance indicated that year and parity differences were not significant, with differences mainly due to age (Table 6). Overwintered females had larger litters than young females. Second litters were also marginally larger in overwintered females, but were smaller in young females (Table 6). The increase in litter size from the first to the second litter in overwintered females may be slightly exaggerated, as a small number of third litters were probably mistakenly classified as second litters. Embryo mortality prior to and just at birth (difference between placental scar counts and counts of young at parturition) was 2.4%, and did not differ between years ($X^2=1.26$, $P > 0.25$). Nestling mortality from birth to weaning on day 21 was 3.6%, and also did not differ between years ($X^2=1.74$, $P > 0.1$).

With the extensive trapping on the multiple capture grid, I was able to follow the life histories of mature females. From data on weight changes, nipple development, and the opening of the pubic symphysis, I estimated the number of litters born. This estimate is given with confidence limits representing a lower bound for litters that were unquestionably born (large weight changes, litters in traps, wide open pubic symphyses, prominent nipple development), and an upper bound for litters that may have been born (females that were close to parturition at last capture, females that had prominent nipples on first capture). This method suggests that 28 to 33 litters were born in 1976, and 29 to 30 litters were born in 1977. A cruder estimate was also calculated from an independent set of parameters:

$$\text{No. Litters} = \frac{\text{Pregnancy rate X Length of breeding season X Mean No. mature females}}{\text{Gestation period}}$$

This method suggests that 36 litters were born in 1976, and 32 were born in 1977. These estimates are slightly higher than the observed estimates because this calculation counts short-lived females in the average even though they cannot produce a litter unless they live for at least 22 days.

The similarity in total reproductive output between years was also confirmed in the data from general trapping. Pregnancy and birth were determined absolutely, and did not have to be estimated. In total, 51 litters were born for 8,064 trap nights in 1976, and 46 for 8,288 trap nights in 1977 (0.63 vs 0.55 pregnancies / 100 trap nights). Overwintered females produced 75 and 78% of the litters in 1976 and 1977.

Recruitment

The number of young captured on the multiple capture grid differed considerably between years (Fig. 2). Young were first caught at a mean weight of 16.7 g in 1976, and 17.1 g in 1977 ($t=1.14$, $df=203$, $P > 0.2$). Young were therefore about the same age at first capture in each year (roughly 30 days). Juvenile survival rates (birth to trappable age) were calculated for each year from the estimates of the number of litters born on the grid, and the estimates of litter sizes from litters born in captivity:

$$\text{Survival} = \frac{\text{No. Young Captured}}{\text{No. Litters X Litter Size}}$$

Juvenile survival was 86 to 102% in 1976, and 29 to 30% in 1977.

The fact that juvenile survival exceeded 100% in 1976 probably reflects an overestimate of recruitment into the trappable population rather than an underestimate of the number of litters born. The grid was located within a large area of suitable habitat for *Clethrionomys gapperi* (Wells

1976), and therefore probably sampled some dispersing individuals. Dispersal in increase and peak populations of microtines is common (Krebs and Myers 1974), and was evident in 1976 on removal grids run at Heart Lake (Doyle 1979). If I exclude recruits caught only once from the calculation of juvenile survival (possible transients), then survival estimates become 64 to 76% for 1976, and 28 to 29% for 1977.

Age Structure

For this analysis and others, each year was divided into six time periods based on female reproduction (Table 7). Median dates were used to divide the season rather than mean dates for two reasons. First, errors in parity assignment due to the disappearance of placental scars resulted in extremely unusual dates for some litters. These litters had a considerable effect on the average date of birth for any particular category, but had a much smaller effect on the median date. Second, I felt that meaningful transitions in demography and behavior would probably be detected when at least half of the population was involved in the same reproductive activity.

Differences in juvenile survival resulted in different age structures in 1976 and 1977 (Table 8). Open and closed groove age-classes (about 20 to 60 days of age) formed a smaller proportion of the population in periods 4 and 6 of 1977, indicating that juvenile survival may have differed between years only early and late in the season. At mid-season, the catch of overwintered voles was very low in 1977

(1976: 1.70/100 trap nights; 1977: 0.25/100 trap nights), possibly accounting for the high proportion of young age-classes in the sample. Since a similar decline in overwintered density was not observed on the multiple capture grid, it is not clear whether this decline was general or local.

The fall populations were composed of animals born at different times in each year. In 1976, M^2 tooth measurements (see section on ageing captive voles) showed that 90% of the open and closed groove age-classes were born in period 5. In 1977, 23% of these age-classes were born in period 5, whereas the rest were born in period 4. A similar influx of young voles late in the season was also observed on the multiple capture grid in 1976 (Table 9). The probability of each successive wave of recruits surviving to the fall varied slightly between years, but sample sizes were too small to show any significant differences. If survival after recruitment actually did vary between years, it would have had a minimal effect on age structure, considering the large number of animals recruited in 1976.

The age structure of overwintered voles was analyzed by an Analysis of Covariance of the regression between M^2 root length and date of autopsy. Males and females were first compared and no significant differences in the regressions were found. Year differences were then analyzed (Table 10). Intercepts were found to be significantly different, indicating that the mean age of overwintered animals was lower in 1977 than in 1976. Animals were about two weeks younger assuming a root growth rate of about 0.14 mm per month (Table 10). This may have reflected a difference in physiological age (different root growth rates in the preceding winter), or chronological age (variable fall age structure or differential winter mortality). Since animals were particularly young in the fall of 1975 (Fuller, unpublished), this difference probably reflected differential root growth or differential mortality.

Sex Ratio

Deviations from a 1:1 sex ratio were analyzed by X^2 tests on data combined from the multiple capture grid and Sherman traplines (Table 11). This was necessary because of small sample sizes, and the possibility of differential trap response between the sexes. Data sets did not differ in any period (X^2 tests). Sex ratios in overwintered voles and young mature voles were even. Sex ratios in immature young were consistently biased towards males, but this bias was only significant in periods 5 and 6 of 1976, and period 6 of 1977.

Sex ratio at birth was 1:1 (116:116), as was the ratio in young voles in the open groove age-class (Table 12). Sex ratios at first capture on the multiple capture grid were biased towards males in immature voles, but not in mature voles. Sex ratios in the closed groove age-class were also biased towards males in immature voles, but not in mature voles. Sex ratios therefore became biased at an age of about one month, but only in immature voles. In rooted mature voles (age >2 months), sex ratio was biased towards females (Table 12). Since there is a slight excess of mature males in open and closed groove age-classes, females may simply develop roots at an earlier age than males. The complementary sex biases in mature and immature voles may be due to differential sexual maturity (Kalela 1971), but this explanation does not account for the overall excess of males in the population (194M: 135F). In particular, the male-biased sex ratio in immature voles born late in the season is inconsistent with Kalela's explanation, since none of these animals mature. Differential mortality between the sexes early in life may account for this difference, although there are many possible explanations (Myers and Krebs 1971a).

Early-spring overwintered sex ratios reflected male-biased sex ratios in fall (e.g. period 6 (1976): 63% M, period 1 (1977): 59% M), but sex ratios tended to equalize in later periods (Table 11). Since more overwintered females are caught per unit effort as spring progresses (Fuller, unpublished), the early-spring male-biased sex ratios may simply reflect low female trappability. If this is the case, actual sex ratios in early-spring may be even, indicating that males suffer higher mortality in winter than females.

Summary

1. There was an eight-fold increase in density from spring to fall in 1976, and a three-fold increase in 1977.
2. Nearly the same number of animals survived the winters of 1976-77 and 1977-78 from fall densities which differed by a factor of 3.8.
3. Total production cf young was about 15% higher in 1976 than 1977.
4. High levels of recruitment in 1976 were mainly the result of good survival from birth to trappable age.
5. Good juvenile survival resulted in a young age structure in 1976.
6. Overwintered animals were about two weeks younger in 1977 than in 1976.
7. Sex ratios were biased towards males in immatures at an age of about one month, and were biased towards females in mature young at an age of about 2 months.

5

Captive Voles

Ageing

In animals raised in captivity the anterior labial groove of the second upper molar (M^2) closed between 32 and 35 days of age, and measurable roots formed between 62 and 72 days (Fig. 3). The proportion of animals with the groove just closing (index of groove closure= 0.1 mm), and the groove well closed (index > 0.1 mm) was compared among population categories by X^2 tests on data lumped over 5-day intervals. Groove closure was independent of the parity or age-class of the mother (OW or YG), and the sex or sexual maturity of the individual.

The best estimators of age were determined by performing a stepwise multiple regression analysis of age with the following variables:

(1) corrected weight (pregnant females: total weight - weight of reproductive tract, others: total weight)

(2) body length (total length - tail length)

(3) M^2 tooth measurements (tooth length, index of groove closure, index of groove closure / tooth length)

(4) logarithms of the above variables.

The best regressions were found between age and tooth length and the logarithm of the index of groove closure (Table 13), although all of these variables were significantly correlated with age. Tooth length increased with age until the time of groove closure, and then decreased. The regression for mature animals was only marginally significant, mainly as a result of large deviations on the part of a few animals. When applied to wild-caught voles, these regressions estimated their ages between 16 and 68 days.

Moult pattern could also be used as a crude indication of age (Fig. 4), although it was not used in this study. The patterns shown in Fig. 4 do not represent all of the patterns seen in wild voles, and probably represent more than one moult between 20 and 60 days of age.

Most voles born early in the season (both males and females) developed a moult on the flank glands from 48 days of age onwards (21 or 91% of these voles were mature). Attempts at histological identification of flank glands with oil blue N stain (Quay 1954) were unsuccessful (most of the skins obtained in 1976 were stained). I do not know whether this represents poor technique, or a genuine lack of flank gland activity in subarctic Clethrionomys gapperi. Externally visible flank glands and scent marking behavior (Skirrow and Ryšan 1976) were seen in wild-caught voles with and without a moult on the flank glands.

Pigmentation of the perianal pouch (Stewart and Brooks 1977) was noted in both captive and wild-caught mature males. All captive mature males had pigmented pouches that were often visible as early as 21 days of age. Four captive immature males born in late June and autopsied at an age of about 40 days also had pigmented pouches. These few males may represent animals that are inhibited from attaining sexual maturity (Kalela 1957) due to interactions with adult males (Viitala 1977). If this hypothesis is correct, immature voles could be scored for the presence of the perianal pouch to differentiate between those animals behaviorally inhibited from attaining sexual maturity and those animals genetically destined not to mature.

Sexual Maturity

Animals born early in the season matured at an early age. Many males had descending testes when weaned on day 21, and had fully scrotal testes when checked in the pens a week or two later. One male autopsied at 22 days was mature (sperm present in the epididymides and testes). Females all had imperforate vaginas when weaned on day 21. Two females had placental scars when autopsied at 50 and 53 days of age. Four females had embryos that would have been born at 43, 47, 56, and 59 days. Given a 22 day gestation period, females must have attained sexual maturity between 21 and 37 days of age.

Attainment of sexual maturity was mainly related to the date of birth. All animals born before 19 June matured, and all animals born after 4 July did not mature (Fig. 5). Only animals autopsied at an age of at least 40 days were considered in establishing the above limits. Animals born in the transitional period were exposed to shortening day lengths as nestlings, possibly triggering physiological mechanisms that inhibit maturity (Clarke 1977). During the transitional period it was impossible to determine which animals would mature. Males and animals from second litters were less likely to mature, but neither of these trends was significant ($X^2=1.71$, $P=0.25$; $X^2=1.35$, $P=0.53$). Similarly, animals that matured or did not mature were the same weight at weaning ($t=0.63$, df=56, $P=0.53$). Since the earliest litter of a wild-caught young vole was born on 15 July (Table 5), it is obvious that only young of overwintered females matured in 1976 and 1977.

Sex Ratio

Although the overall sex ratio at birth was even (116M: 116F), there was a suggestion of temporal variation. If the year is divided into three periods based on the attainment of sexual maturity (all animals mature, some mature, none mature), then there is a bias towards males in animals born in the first two periods, and a bias towards females in the last period ($X^2=3.92$, df=2, $P=0.14$). This late-season female bias is opposite to the male-biased sex ratio in wild-caught immature voles (Table 11 & 12), and is related to a trend for first litters to be male-biased, and second litters to be female-biased. These trends are only significant in second litters born in the period when no animals mature (48F: 29M, $X^2=4.21$, $P < 0.05$).

Growth

Animals raised in captivity reached abnormally high weights in comparison with wild-caught voles. Captive voles often weighed as much as 30 to 40 g at 50 days of age. Much of this weight was in the form of large quantities of subcutaneous fat, probably accumulated after weaning, since weights at weaning were not particularly high [14.56 g ± 0.136 (SE)]. Captive voles also grew slightly faster than their wild counterparts (Captive voles: Body length= 83.2 mm + 0.27 Age in days, $r^2=0.34$; Wild-caught voles: Body length= 82.3 mm + 0.18 Age in days, $r^2=0.17$). Since there were some obvious differences between the pattern of growth in captive and wild-caught voles, the following results should be interpreted with caution.

Factors affecting growth were analyzed by stepwise multiple regressions of four growth variables with a number of factors. Due to possible qualitative differences in the growth characteristics of young from different phases in the population cycle (Fuller 1977b), only the data from 1977 were included in this analysis. Growth was described by weight at weaning, weight gained after weaning, body length, and condition (Table 14). The 14 variables used in the appropriate regressions were:

(1) mean minimum and maximum temperature during the first 21 days of life

(2) mean minimum and maximum temperature during the time spent in the pen

(3) age-class of the mother (OW or YG)

(4) parity of the mother (first, second, third litter)

(5) litter size

(6) corrected weight, body length, and condition (defined in Table 14) of the mother at weaning

(7) day of the year at birth

(8) age in days or number of days in pen

(9) sex

(10) maturity

(11) transferrin phenotype (see section on electrophoresis) entered as a dummy variable relative to the heterozygote.

Weight at weaning was significantly related to litter size, condition of the mother, and day of the year at birth (Table 14). Animals from small litters, litters born late in the year, and litters with a mother who was in good condition at weaning, were heavier on day 21. After weaning, weight gain was mainly a function of age (accumulation of fat), although males gained less weight than females. Animals that were weaned at a heavy weight also gained less weight after weaning. Length was mainly related to age, although the Slow-Slow transferrin phenotype grew at a slower rate than the other two phenotypes. Condition reflected the combined patterns in these three variables, and was mainly related to age and weight at weaning. Smaller effects due to sex and transferrin phenotype were also significant.

Some variables did not enter into the regressions because they were highly correlated with other variables that explained larger proportions of variance. For example, minimum and maximum temperatures during the first 21 days of life were significantly negatively correlated with weight at weaning. Temperature variables nevertheless did not enter into the regression since large litter sizes, high values of condition in the mother, and low values of day of the year were simultaneously related to high minimum and maximum temperatures. Similarly, overwintered females weaned larger young, but the overwintered females were also in better condition than young females.

One unexpected finding was the lack of significant differences in growth between mature and immature individuals. Synergistic relationships between maturity and other variables were not evident as in the case of temperature variables. Animals born late in the year were actually weaned at heavier weights than animals born early in the year, and also continued to grow while they were in the pen. This is opposite to the small size and inhibited growth of immmature animals born late in the year in field populations (Stebbins 1976, Fuller 1977b). It is also interesting that growth was stimulated by the high nutritional plane, but sexual maturity was not (Andrzejewski and Mazurkiewicz 1976). Failure to mature on the high nutritional plane reinforces the conclusion that inhibition of maturity was due to the light regime.

Summary

1. Ages of animals can be estimated with a mean absolute error of 2 to 4 days up to about 70 days of age by means of regressions based on M^2 tooth measurements.
2. Only animals born to overwintered females before 4 July matured in 1976 and 1977.
3. A short transitional period existed for about two weeks at the time of the summer solstice when it was impossible to predict which animals would mature.
4. Growth patterns in animals maintained in captivity on rodent chow deviated considerably from those observed in the field, in spite of the semi-natural conditions under which they were raised. Variables reflecting different aspects of growth were related to age, sex, transferrin phenotype, day of the year at birth, litter size, and condition of the mother at weaning.

Social and Behavioral Structure

Frequency of Multiple Captures

In total, 22.9% of all captures of *Clethrionomys gapperi* on the multiple capture grid were multiple captures, i.e. at least one other individual was present in the trap at the same time. Three voles were trapped together simultaneously 16 times, and four voles were trapped together twice; the remaining multiple captures were double captures. About 71% of the population was involved in multiple captures. Animals that were not taken in multiple captures were only captured a few times. Signs of wounding (broken tails, cuts, gashes, lost toes, lost fur) were rare (0.6%), and were equally distributed between single and multiple captures ($X^2=0.02$, $P > 0.75$).

Involvement in multiple captures was mainly related to sexual maturity. Immature voles were involved in significantly more multiple captures than mature voles (38% vs 16%, $X^2=149.21$ $P \ll 0.001$). Males and females were equally likely to be involved in multiple captures (Mature: 17% vs 15%, $X^2=0.84$, $P > 0.25$; Immature: 39% vs 38%, $X^2=0.01$, $P > 0.9$). Overwintered voles and young mature voles were also equally likely to be involved in multiple captures (15% vs 16%, $X^2=0.45$, $P > 0.5$). Similar patterns were observed in both 1976 and 1977.

In any given rota, the frequency of multiple captures was mainly a function of numbers. For example, the proportion of multiple captures in each rota was related to the number of animals known alive as follows:

$Y=0.099 + 0.0033\ X\ (r^2=0.64)$.

When young of the year were present in the population (rotas 5 on), this relationship was particularly strong:

$Y=0.097 + 0.0033\ X\ (r^2=0.88)$.

A computer simulation of random captures on a grid of 121 stations with 50% trappability produced a similar relationship: $Y=0.0032\ X$. This relationship between the proportion of multiple captures and numbers partially accounts for the high proportion of multiple captures in immature voles (which live at higher densities than mature voles). Sample sizes were unfortunately too small to do an Analysis of Covariance of this relationship between mature and immature voles.

Two other indices of space-related behavior were also calculated for each rota:

1. Proportion of spatial overlap (number of trap sites visited by more than one animal/ number of trap sites visited by all animals),

2. Proportion of trap visitation (number of trap sites visited by all animals/ number of trap sites on the grid).

These two indices were highly intercorrelated with the proportion of multiple captures (mean $r=0.8$), and were also significantly related to numbers:

Spatial overlap$=0.33 + 0.0035\ X\ (r^2=0.71)$,

Trap visitation$=0.26 + 0.0050\ X\ (r^2=0.66)$.

These equations show that animals were caught at more trap stations on the grid as population density increased, and also overlapped more in the areas that were being used. Therefore, an increase in the proportion of multiple captures at progressively higher population density presumably reflected an increase in spatial overlap, rather than an increase in the "attraction" between animals.

These relationships between spatial behavior and density were summarized by performing a Principal Components Analysis of the three indices. About 80% of the variance in the first principal component ($Y=0.82$ Prop. multiple captures + 0.92 Prop. spatial overlap +0.92 Prop. trap visitation, Eigenvalue=2.15, % Variance=71.6) was accounted for by the number of animals known alive on the grid (Fig. 6). This relationship showed a slight indication of curvilinearity ($r^2=0.86$ if one takes the log of numbers rather than numbers). Although I have very few observations at high density, the data suggest that overlap in space may reach an asymptote at very high densities.

Patterns in Multiple Captures

Randomness of association in multiple captures was tested by comparing the observed distribution of multiple captures to the distribution expected on the basis of chance alone (Slade 1976). Sample sizes were large enough for analysis in double captures only. Sexual combinations in double captures of immatures did not deviate significantly from randomness (Table 15). In contrast mature voles were more likely to be caught with mature voles of the opposite sex, than of the same sex (Table 15). This trend was also evident in multiple captures of mature voles with immature voles in 1976 (Table 16). Based on a small sample, captures of mature voles with immmatures in 1977 appeared to be random (Table 16).

Spatial Patterns

Some of the variation in the frequency and pattern of multiple captures was related to spatial organization. Various Minimum Area Home Ranges (Stickel 1954) in 1976 and 1977 are shown in Fig. 7 & 8. Overlap in these two figures is slightly exaggerated since all individuals were not alive at the same time, and individuals were not necessarily caught at all points within their ranges in any one rota.

Overwintered and young mature females maintained exclusive home ranges or territories among themselves in both 1976 (Fig. 7A) and 1977 (Fig. 8A). Although the ranges of a few mature females in these two figures overlap in space, very few of these ranges actually overlapped in time. There were only 15 cases of two mature females caught at the same trap site in one rota. The infrequency of multiple captures of mature females (Table 15) was presumably related to this lack of spatial overlap.

Mature males contrasted with females in that their home ranges overlapped extensively with those of other mature males [Fig. 7B & 7D (1976), Fig. 8B (1977)]. Captures of two or three mature males at one trap site in one rota were common, with up to six animals at one site in the spring of

1976. Despite considerable spatial overlap, multiple captures of mature males were nearly as infrequent as those of mature females (Table 15). This presumably reflected a temporally fine-grained behavioral structure in the mature male population, as space on a long time-scale (i. e. home range) was shared, whereas space on a short time-scale (i. e. day to day movements) was used exclusively. Maintenance of this system would presumably require some short-term advertisement of an animal's presence, either through scent marking or behavioral interactions.

Home ranges of overwintered males were very large (Fig. 7B), indicating that the 6.25-ha grid was probably too small to adequately estimate their movements (Wells 1976). This was particularly evident in the first few rotas of each year, when individual overwintered males typically had home ranges encompassing a large proportion of the grid. Overwintered males ranged widely on a relatively short time-scale as well, moving between 50 and 100 meters between captures on average.

Immature males and females had small, moderatley exclusive ranges (Fig. 7C, 8C, & 8D). Immatures appeared to settle into areas that were not occupied by mature females, and I could therefore not associate any particular individual with its possible mother. Multiple captures of immatures were nevertheless relatively common (Table 15), even though home ranges did not appear to overlap extensively.

The significance of these spatial patterns was tested by performing a nearest neighbor analysis (Clark and Evans 1954) of centers of activity (arithmetic mean of capture locations) of animals captured in each rota (Table 17). Centers of activity of reproductive males and immatures were randomly distributed in nearly every case. In contrast, centers of activity of reproductive females were typically uniformly distributed, with 10 of 17 comparisons significant. Interactions between the spatial patterns of different segments of the population occasionally resulted in nonrandom distributions in the population as a whole (e.g. rota 1 of 1978).

Capture frequencies at trap sites in each rota were also compared with distributions based on chance by the "intensity of contacts" method of Bujalska (1970, page 395). This method compares the frequency of captures at trap sites visited by one, two, three, etc. animals, with the frequency expected on the basis of chance alone. Multiple use of trap sites was common only in immatures and in reproductive males as noted previously. No significant deviations from a random distribution were detected, indicating that the catch at trap sites was independent of the number of animals visiting the trap sites.

Association Patterns

To summarize the behavioral structure of the population, I performed a taxonomic analysis of multiple captures. For each year, I constructed a similarity matrix between animals involved in multiple captures. Two animals caught together at any time were assigned a similarity of 1, whereas two animals not caught together were assigned a similarity of 0. This matrix was then analyzed by the unweighted pair group method (UPGMA) of Sokal and Michener (1958).

The dendrograms for both years were highly chained and lacked any striking evidence for group structure (Fig. 9). Clusters at high levels of similarity were small, reflecting the infrequency of reflexive multiple captures (e.g. A was caught with B and C, but B was rarely caught with C). I could not identify any consistent pattern in the composition of clusters. Animals were simply caught with some of their neighbors (especially of the opposite sex). Clusters mainly represented spatial and temporal overlap between animals.

To show the pattern of contacts I have selected some long-lived individuals and delineated their multiple capture histories in Fig. 10 and 11. Each horizontal bar in the diagrams represents the length of time an animal, involved in a multiple capture with the selected individual, was known to be alive. Each dot represents a multiple capture with the selected individual.

Mature females were almost exclusively caught with mature males throughout the main breeding season, and were only caught with other animals late in the season (Fig. 10 & 11). For example, overwintered female No. 22 (Fig. 11) dropped four litters in 1977, but was only caught with two immature males in rotas 9 and 10. In general, mature females were rarely involved in multiple captures, and were rarely caught with the same individual more than once or twice. Mature males were also rarely involved in multiple captures, but were caught with a larger variety of animals than mature females (Fig. 10 & 11). Mature males were captured with different mature males and females throughout the season, with the occasional repeat capture. As in mature females, captures with immatures only occurred towards the end of the breeding season.

Animals that lived relatively close to each other were often involved in multiple captures with different animals. For example, the centers of activity of female No. 22 (cluster A, Fig. 9) and male No. 106 (Cluster B, Fig. 9) were 67 m apart (population mean Adjusted Range Length is 154 m), but these animals were only involved in multiple captures with two individuals in common (Fig. 11).

Immature voles were only censused for a relatively short time in each year, and I therefore have no long capture histories for immatures. Immatures were generally involved in multiple captures with a wide variety of animals with few repeat captures. The longest record consists of immature male No. 90 who lived from rota 6 to rota 10 of 1976. He was caught with a mature male, two mature females, six immature males, and two immature females, with only three repeat captures in his lifetime. Similarly, immature female No. 23 lived from rota 8 to rota 10 of 1977, and was caught with one mature male, and three immature males, with two repeat captures.

Summary

1. Mature females lived within mutually exclusive areas (territories) throughout the season, and were rarely involved in multiple captures with animals other than mature males.
2. Mature males inhabited large, extensively overlapping home ranges, and were involved in multiple captures with an assortment of individuals.
3. Immatures had small, moderately exclusive home ranges, and were often caught with other immatures, but were only caught with mature voles towards the end of the breeding season.
4. Patterns of association revealed no evidence for any lasting bonds between animals, including mature females and young.
5. The behavioral and spatial structure of the population was similar in both 1976 and 1977.

Growth

Weight

Mean weights of animals captured on the multiple capture grid were similar in 1976 and 1977 (Fig. 12). Note that sample sizes for nearly all of the points in Fig. 12 are small (typically < 10 individuals). Overwintered males attained full weight before May in each year, and did not gain weight through the summer. Overwintered females were slightly lighter than males in May, but continued to gain weight through the summer until they were much heavier than males. Based on very small samples, both sexes appeared to lose weight in the latter half of 1976. A smaller weight loss may also have occurred in 1977.

Samples for young mature individuals were particularly small. Young mature males and females were lighter than overwintered animals, but there was some overlap in the distributions. Immatures were much lighter than mature animals, and showed no apparent sexual, seasonal, or yearly differences.

Gross weights at capture of overwintered voles caught on Sherman traplines were regressed with the date of capture in each year. Overwintered males did not increase in weight significantly through 1976 ($F=0.01$, df=48, $P=0.09$), but may have increased slightly in weight in 1977 ($Y=21.6$ g $+ 0.014$ Day of year, $F=4.45$, df=66, $P=0.04$). Note that overwintered males caught on the multiple capture grid did not show a similar increase in weight in 1977. When I lumped overwintered males caught on Sherman traplines through the entire season, I could not detect any difference in weight between years (1976: 24.5 g, 1977: 24.1 g, $t=0.77$, $df=117$, $P=0.6$).

Overwintered females gained weight only in the first half of the season (Fig. 12). Regressions for overwintered females caught before 1 July indicated considerable growth in each year (females < 8 days to parturition excluded):

1976: $Y=0.6\text{ g} + 0.154$ Day of year ($r^2=0.37$),

1977: $Y=0.3\text{ g} + 0.152$ Day of year ($r^2=0.62$).

An Analysis of Covariance indicated that these regressions were not significantly different (equal slope: $P=0.97$, equal intercept: $P=0.58$).

Weight at capture was also regressed with an estimate of age at capture in overwintered animals (molar root length at autopsy - 0.0046 days to autopsy from capture). These regressions only explained a small proportion of the variance ($r^2 < 0.10$), and did not differ between years (Analysis of Covariance). Logarithmic transformations of weight or root length or both variables did not improve the relationship. The overall relationship between weight at capture and molar root length in overwintered animals was:

$Y=20.9\text{ g} + 3.73\ X$ ($r^2=0.06$).

Growth in weight in young of the year caught on Sherman traplines was analyzed by regressing gross weight at capture with estimated age at capture (based on M^2 tooth measurements for open and closed groove age-classes).

Results of regressions were highly variable among population categories (Appendix 2), possibly reflecting real differences in growth patterns, or poor estimates of age. Regressions were highly significant only for immature females in 1976 and 1977. An Analysis of Covariance indicated that these regressions were not significantly different (equal slope: $P=0.54$, equal intercept: $P=0.09$). Regressions for immature males explained little variance despite large sample sizes. In particular, there was no significant relationship between weight and age in immature males in 1977. Since these regressions are mainly based on animals in the closed groove age-class (83% of the sample), this may have reflected an early completion of growth in weight in 1977.

Length

Body length at autopsy (total length - tail length) was regressed with the date of autopsy for overwintered animals in each year. Growth in length was presumably affected by captivity, and it is therefore not known how applicable these results are to the field situation. Overwintered males did not increase in length through 1976 ($F=0.03$, $df=42$, $P=0.86$), but probably did increase in length through 1977 ($Y=94.8$ mm $+ 0.038$ Day of year, $F=11.16$, $df=54$, $P=0.002$, $r^2=0.17$). Overwintered females increased in length through the season in both years:

1976: $Y=92.9$ mm $+ 0.067$ Day of year ($r^2=0.15$),

1977: $Y=93.8$ mm $+ 0.063$ Day of year ($r^2=0.18$).

An Analysis of Covariance indicated that these regressions were not significantly different (equal slope: P=0.91, equal intercept: P=0.79). Logarithmic transformations of each variable or both variables did not improve the relationship between length and day of the year. I was also unable to detect seasonal variation in growth in length, due to the small number of animals autopsied before 1 July.

Body length was also regressed with molar root length at autopsy for each sex in each year. No significant differences were found among groups (Analysis of Covariance), and the relationships were generally as poor as those between weight and root length. The overall relationship between body length and molar root length in overwintered animals was:

$$Y=94.8 \text{ mm} + 6.50 X \quad (r^2=0.12).$$

Growth in length in young of the year was analyzed by regressing body length at autopsy with estimated age at autopsy. Regressions between length and age were as variable as those between weight and age (Appendix 2). Regressions for immature males were significant, and may have differed slightly between years (equal slope: P=0.07, equal intercept: P=0.09). The regression for immature females in 1977 was highly significant, but the regression for immature females in 1976 was not. Immature females may therefore have completed growth in length at an earlier age in 1976 than in 1977.

Summary

1. Overwintered males did not increase in weight or length in 1976, but may have increased in weight and length in 1977.
2. Overwintered females increased in weight and in length in May and June in 1976 and 1977. In July and August, overwintered females began to decrease in weight but continued to grow in length.
4. Weight and length of overwintered animals were marginally related to age.
5. Regressions between weight and age, and length and age in young of the year were only marginally significant in most population categories.
6. Immature males may have completed growth in weight at an earlier age in 1977 than in 1976.
7. Immature females may have completed growth in length at an earlier age in 1976 than in 1977.

Wounding

Data on wounding represent animals caught in the Heart Lake area in 1976 and 1977 by various researchers using various methods. Animals were caught on permanent grids and on index lines in Sherman, Longworth, Museum Special, pitfall, and multiple capture traps. I personally scored wounding for all of the skins obtained from various researchers.

Frequency counts of both light and severe wounds were skewed to the right, i.e. many animals had no or few wounds. Light wounding was sufficiently variable for parametric analysis after applying a square root transformation (Sokal and Rohlf 1969, page 384). Severe wounding was rare, and was therefore transformed into a dichotomous variable (absent or present).

Both types of wounding were first tested for possible disappearance in animals held in captivity. Rose and Hueston (1978) found that manually inflicted wounds disappear in *Microtus pennsylvanicus* within about three weeks. In this study, I could not detect any heterogeneity in wounding over a 21-day period from capture to autopsy (Light: F=0.78, df=20, 381, P=0.73; Severe: X^2=16.1, df=20, P=0.80). Nevertheless, I arbitrarily excluded all voles from wounding analyses if they were autopsied more than 14 days from capture.

Temporal Variation

The degree of wounding was mainly a function of year and sexual maturity (Fig. 13 & 14). Severe wounding was uniformly high in all mature animals regardless of age or sex in 1976, and was uniformly low in all animals in 1977, and in immatures in 1976 (Fig. 13). Light wounding was also uniformly low in all animals in 1977, and in young of the year in 1976 (Fig. 14). In 1976, overwintered animals had more light wounds than mature young of the year, which in turn had more light wounds than immature young of the year. Relatively high levels of light wounding were only observed in overwintered animals in 1976, with a significant drop in wounding in the following year.

Within each year, there was some temporal variation in wounding. Severe wounding varied between time periods (Table 7) in overwintered animals in 1976 (Males: X^2=20.9, df=5, P=0.0008; Females: X^2=20.9, df=5, P=0.0008). The proportion of overwintered animals with severe wounds for periods 1 to 6 of 1976 was: 0.13, 0.24, 0.57, 0.57, 0.26, 0.00. Light wounding also varied temporally in mature animals in both years (Fig. 15). Although there was some heterogeneity between different sex and age groups, wounding appeared to be highest during periods 4 and 5, the time of peak breeding intensity, when numerous young of the year were potentially recruiting into the trappable population.

Relationships with Age and Size

Light wounding significantly increased with age [Young: $F=28.1$, df=2,796, $P \ll 0.001$ (based on open groove, closed groove, roots formed M^2 classes); Overwintered: $F=5.25$, df=7,101, $P \ll 0.001$ (based on molar root length classes)]. In contrast, severe wounding was not related to age [Young: $X^2=0.95$, df=2, $P=0.62$; Overwintered: $X^2=5.87$, df=7, $P=0.56$). These relationships suggest that light wounds represent older wounds that have healed and accumulated with time, whereas severe wounds represent relatively fresh wounds. If this interpretaticn is correct, then light wounds reflect the history of wounding in an individual, whereas severe wounds represent an instantaneous sample of wounding.

Both types of wounding were related to size. Animals with severe wounds averaged 3.6 g heavier ($F=54.8$, df=1, 871, $P \ll 0.001$), or 5.7 mm longer ($F=56.2$, df=1, 871, $P \ll 0.001$) than animals without severe wounds. Only animals autopsied within three days of capture are included in these analyses. These trends were consistent within all age, sex and maturity categories in 1976, but were not significant in any groups in 1977. This lack of statistical significance in 1977 was simply the result of the small sample (large variance) of animals with severe wounds in 1977.

The number of light wounds was also positively correlated with size (Corrected weight: $r^2=0.18$, Body length: $r^2=0.16$). This relationship was significant in most subcategories of the population, but was extremely weak.

Overwintered females in 1976 were the only ones to show a moderately high correlation between light wounding and size (Weight: R=0.58, Length: R=0.47). Using molar root length as an index of age in overwintered animals, I compared the relative contributions of size and age towards explaining the variance in light wounding. A multiple regression of wounding with molar root length and corrected weight indicated that most of the variance in wounding was actually related to age ($r^2=0.18$), with only an additional 2% of the variance explained by weight. A regression of light wounding with age and length showed that an insignificant proportion of the variance was explained by length after removing the effects of age. These trends suggest that correlations between light wounding and size are mainly artifacts of the accumulation of wounds with age.

Summary

1. Light and severe wounds probably represented old and new wounds, thereby providing both a history of wounding and an instantaneous sample of wounding.
2. Both types of wounding were very low in all animals in 1977, and in immatures in 1976.
3. Overwintered females had the highest levels of wounding, followed by overwintered males, and young mature animals of both sexes.
4. Seasonal variation in wounding indicated a peak in wounding in July and August in overwintered animals.
5. Animals with wounds were generally larger than those without wounds.

Electrophoresis

Canham and Cameron (1972) detected two alleles at the transferrin locus in Clethrionomys gapperi captured in the Heart Lake area from 1966 to 1968. These results were confirmed in this study with the aid of polyacrylamide gel electrophoresis, which generally provides better resolution of serum proteins than starch gel electrophoresis. Transferrin was resolved into two bands; a slow (S) or cathodal band migrating at a modal distance of 0.49 units relative to the leading edge of the albumin band, and a fast (F) or anodal band migrating at a distance of 0.53 units relative to albumin. A third allele was also found in the heterozygous state in two animals, and was represented by a very slow (VS) band migrating at a distance of 0.47 units relative to albumin (Plate 1: Note that "MIX" refers to the actual mixing of blood from two animals to show that three different alleles are present). Each major band was sometimes accompanied by an anodal trace band that stained weakly (Slow: 52%, Fast: 38%), and usually disappeared within a few days.

Gene frequencies at the transferrin locus have varied from year to year since studies began in 1966 (Table 18), but have not been closely related to changes in population density (Fig. 16). Based on very small sample sizes, correlation coefficients calculated between gene frequency and demographic indices (Appendix 3) indicate the possibility of a negative relationship between the frequency of the fast allele and population density. High frequencies of the fast allele in overwintered animals are correlated with low May and August densities in the current year, and high frequencies of the fast allele in young of the year are correlated with low May and August densities in the preceding year. Since these correlations are based on large changes in gene frequency in only one or two years, these relationships may not be reliable.

Gene frequency changes since 1975 are illustrated in Fig. 17. Time periods for 1975 were arbitrarily set as the average of the periods observed in 1976 and 1977 since intensive live-trapping did not begin until mid-June in 1975. The frequency of the fast allele declined from spring to fall in the 1975 and 1977, and increased in the peak year (1976). The frequency of the fast allele also increased in all three winters of observation.

The significance of these changes was first analyzed by comparing gene frequencies between the sexes separately in overwintered, young mature, and young immature voles in individual time periods (raw data in Appendix 4). None of the X^2 values was significant, indicating that there was no heterogeneity in gene frequency between the sexes. Temporal variation was tested next, lumping the sexes, and comparing within each category between successive time periods. The only significant shift within categories occurred between periods 4+5 and period 6 of 1977, when the frequency of the fast allele declined from 0.58 to 0.44 in young immature voles ($X^2=4.4$, $P < 0.05$).

Random mating was tested next through the use of Incomplete Family Data (Cooper 1968) from wild-caught females and their litters born in captivity in 1976 and 1977 (Table 19). The three X^2 tests suggested by Cooper (1968) were all not significant, suggesting that matings were occurring at random relative to the transferrin locus.

Selection was next analyzed by comparing observed phenotypic frequencies with expected frequencies calculated from random matings in successive parental generations. Overwintered animals were assumed to be the parental generation for all young mature voles. The parental generation of young immature voles could not be determined accurately due to considerable overlap in the lives of overwintered and young mature voles. Immature voles are born to both of these age-classes, with each age-class giving birth to a variable proportion of this generation in each year. Since the parental type of an immature vole cannot be determined, I estimated the average parental gene frequencies for immatures by weighting gene frequencies for the production of young by overwintered and young voles during the times when immature voles are born. Parental frequencies for immatures were therefore calculated from gene frequencies in overwintered and young mature voles, weighting frequencies for the number of young born to females caught on Sherman traplines after June 19 in each year (the first day a young vole born in captivity did not mature). Since some voles did not mature until an age of 30 to 40 days, open groove age-classes were excluded from analysis in 1976 and 1977. Sample sizes were too small to exclude animals in 1975. Immatures caught in 1975 mainly represented the late-season immature cohort since all but one of them were caught after 8 August.

Given these assumptions, early components of "fitness" were calculated for the early-season "generation" of voles that matures in the year of its birth, and the mid to late-season "generation" of voles that does not mature (Appendix 5 & 6, Fig. 18). "Fitness" here is not equal to Darwinian fitness in the normal sense since it is impossible to compare gene frequencies in successive generations at the same stage in the life cycle due to overlap in overwintered and young breeding. Only the early-season generation represents a distinct group that can be identified with a specific parental generation. These fitness calculations therefore only represent an estimate of each phenotype's ability to survive to trappable age. The true fitness of the phenotypes is unknown, since it is impossible to estimate their relative contribution to successive gene pools.

Significant deviations from expected phenotypic frequencies occurred at four times between 1975 and 1978, presumably reflecting differential fitness among the transferrin types (Fig. 18). Differential trappability under certain conditions may also account for these deviations, but this seems unlikely. The pattern of captures during the four day sequence of general trapping was not significantly different across the three transferrin phenotypes ($X^2=15.6$, DF=12, P=0.2). In 1975, 1976, and 1978, the catch of young mature heterozygotes was higher than expected on the basis of random mating among overwintered voles. This difference presumably reflected a real difference in "fitness" since young immature voles that may have been exclusively born to overwintered parents (determined by ageing animals back to their date of birth by means of M^2 tooth measurements) did not differ in gene frequency from their mature counterparts (1976: $X^2=1.6$, $P > 0.1$; 1977: $X^2=0.17$, $P > 0.5$). In immature voles, intense selection only occurred in late-summer of 1977, when many more immature SS homozygotes were captured than expected (Appendix 6). The summer of 1977 was also characterized by poor juvenile survival, which is consistent with the intensity of selection in young immature voles. These events may have been related to environmental conditions in the summer of 1977. July and August of 1977 had the coldest mean daily maximum temperatures since records have been kept at the Heart Lake Biological Station (1968-1977 range July: 22.5°C - 25.6°C, July 1977: 22.5°C; 1968-1977 range August: 19.5°C - 23.8°C, August 1977: 19.5°C; Fuller, unpublished).

Gene frequency changes over winter were tested by comparing late-season samples (period 5 for 1975, period 6 for 1976 and 1977) with overwintered samples in the following year. Although the frequency of the fast allele increased in each winter from 1975 to 1978, none of these differences was individually significant (1975-76: $X^2=3.30$, $P > 0.05$; 1976-77: $X^2=1.88$, $P > 0.10$; 1977=78: $X^2=0.17$, $P> 0.5$). Significant selection over winter may have occurred in these years, but was difficult to detect since both fall and spring samples represented various generations. At present, there is no way of identifying separate generations in spring samples.

Summary

1. The frequency of the fast transferrin allele decreased in the 1975 and 1977 breeding seasons, and increased in the peak (1976) breeding season.
2. Year to year variation in gene frequencies was indicative of a general negative relationship between the frequency of the fast allele and population density.
3. The frequency of the fast allele increased between fall and spring in three successive winters from 1975 to 1978.
4. Heterozygotes were the most fit phenotype in 1975, 1976, and 1978 in the early-season generation that is born to overwintered animals and matures in the year of its birth.
5. The SS homozygote was selected for in an unusually cold summer in the post-peak year (1977) in the late-season generation that does not mature in the year of its birth. Homozygotes were subsequently nearly absent in the sample of young taken in July 1978, although they were common in the overwintered sample.

Behavior

Altogether, 833 neutral arena trials were staged between wild-caught voles in 1976 and 1977. Only 79% of the trials resulted in at least one encounter between the participants in 1977 as opposed to 85% in 1976 ($X^2=10.6$, $P < 0.005$). I also staged 48 trials between standard voles, and 96 trials between standard voles and wild-caught voles in 1977. In total, these trials represent 4825 encounters (about 6 per 15-min trial) during 236-hr of observation on 500 voles.

Descriptive Inventory

Behavior is described in terms of the English translations of various behaviors documented for *Clethrionomys* in German by Johst (1967). English terminology is the same as in a previous study of behavior in *Clethrionomys gapperi* (Mihok 1976). Behaviors not mentioned in these two studies are described with terminology used in other descriptive studies of rodent behavior (Clarke 1956; Eisenberg 1968; Skirrow 1969; Allin and Banks 1968; Krebs 1970; Turner and Iverson 1973; Skirrow and Ryšan 1976).

In the neutral arena tests, animals noticeably changed their behavior only when they were in visual contact and relatively close to each other (roughly 15 cm). An animal would sometimes pass by an opponent if the opponent was partly buried in the wood shavings that covered the floor of the arena. If an animal detected the other vole, it approached in one of four characteristic ways: elongateelevated approach (*stretch*), head-down, eyes-closed, ears-folded approach (*submissive*), casual approach (*neutral*), and stop-start approach (*hesitant*). In the *stretch* (*Str*: Plate 2) approach ("Streckstellung" of Johst 1967), the body, head and tail form a straight line with the front slightly elevated, the ears directed forward, and the hair on the back erect. The *stretch* approach is sometimes followed by a *sideways movement* ("Seitwärtsbewegung" of Johst 1967) in which the animal circles to the flank of its opponent and subsequently attacks. In the *submissive* (*Sub*: Plate 2) approach, the head is directed down, the eyes are half-closed, and the ears are folded into the contour of the body. This approach is common in *Peromyscus* (Eisenberg 1968), but has not been recorded in studies of microtines. On a few occasions animals may adopt an unusual posture that may be a variation of the *submissive* posture (*Sub*?: Plate 2). This posture resembles the normal *submissive* posture in some respects but has additional components involving the exposure of the flank and part of the underside of the body. Note particularly the prominent flank gland and the curling of the tail under the body in the animal in Plate 2. A somewhat similar posture has been scored as submission in *Peromyscus* (Eisenberg 1968: Fig. 2C).

The *neutral* and *hesitant* approaches represent functional categories rather than specific postures. A *neutral* (*Neu*) approach is represented by a simple continuation of the casual, exploratory movements of the approaching vole. A *hesitant* (*Hes*) approach is characterized by discontinuity; the animal slows down or changes direction, stopping and starting as it approaches. In amicable situations the *neutral* approach is followed by nasal investigation and sniffing (*Nasonasal*: *Nn*) or anal-genital investigation and sniffing (*Nasoanal*: *Na*). In stressful situations (under bright lights, after handling) a vole will often assume a body-tail up posture (*Alert*: Plate 2) similar to the *alert* posture of *Microtus agrestis* (Clarke 1956). In the *alert* posture the entire body is slightly elevated, the hair is erect, the ears are directed forward, and the tail is noticeably elevated. This posture resembles the *stretch* posture but differs in that the tail is sharply elevated and the entire body rather than just the front of the body is elevated. The *alert* posture is also maintained throughout exploration of the arena, whereas the *stretch* posture is only used on approach in encounters with other voles. Furthermore, the *alert* posture is rarely assumed under normal conditions, except during extremely aggressive trials.

During an encounter the most common forms of aggressive behavior include various postures and actions that are generally interpreted as defensive or threat behaviors. Voles will typically "paw lift" ("Pfotenanheben" of Johst 1967) into either a crouching posture ("Kauerstellung" of Johst 1967) or a fully upright posture ("Aufrechtstellung" of Johst 1967) in response to an approaching vole. The crouching posture (*Rap* or *raise partially*: Plate 3 & 4) is particularly variable and can involve many different forms in which the only common feature is the lifting of the paw(s) and the elevated body position. From the *partially raised* posture, an animal will very rarely "stretch" forward into a posture somewhat similar to the *stretch* approach (seen no more than 10 times). This posture resembles "Schnauzenkontrolle" (Johst 1967: Fig. 2), and has therefore been termed *muzzle control* (*Muzzle*: Plate 4). An animal in this position will often raise and lower its body slightly in unison with its opponent in what appears to be a contest for superior elevation between the two animals.

The fully upright posture (*Rai* or *raise*: Plate 3 & 4) is less variable than *Rap*, but has occasionally been divided into offensive and defensive postures based on whether the animal leans towards or away from the opponent (Allin and Banks 1968). When a vole assumes *Rap* or *Rai*, it typically wards off the opponent with one (*Pw1*: *pawbeat 1* or "einseitiges Pfotenschlagen"), or both paws (*Paw*: *pawbeat* or "beidseitiges Pfotenschlagen" of Johst 1967). Pawbeating with a single paw sometimes terminates with the animal hovering over its opponent or resting its paw on the opponent's head while the opponent assumes a *submissive* posture (Plate 3 & 4). In most cases the submissive vole will alternate a *submissive* posture with attempts at investigation (*Nn*, *Na*), which will initiate more *pawbeating* or a *partial raise*. Either vole will sometimes *turn away*

(*Tur*: Plate 3) in response to *pawbeating*. This action roughly corresponds to "Zurückweichen" of Johst (1967) in which an animal draws the head and front part of the body away from the opponent and assumes a hunched, sideways posture relative to the opponent. *Tur* differs from Johst's description in that an animal may *turn away* repeatedly during an encounter without actually withdrawing.

Animals that assume the fully upright position (*Rai*) in defensive encounters usually do not engage in alternate bouts of *Rap*, *Tur*, *Pwl*, and *Sub*; instead they tend to "box" with mutual *pawbeating*. Boxing often leads to fighting in the neutral arena, rather than a retreat on the part of one individual, which is the usual case in the field where escape is possible (Clough 1968). While boxing, animals may dodge each others pawbeats ("Pendeln" of Johst 1967) or occasionally brace against each other with their paws (*Brace*: Plate 3, "Wegstemmen" of Johst 1967). Boxing matches occasionally result in one animal being pushed onto its back ("Rückenlage" cf Johst 1967). This posture has also been termed *supine* (Clarke 1956), *submission* (Krebs 1970), and *submissive* (Turner and Iverson 1973). Voles that are being vigorously attacked and chased will sometimes assume this posture spontaneously.

Intense forms of aggression such as *attack* (*Att*), *chase* (*Cha*), and *fight* (*Fgt*) are rare in *Clethrionomys gapperi* (Mihok 1976). Animals usually attack on approach out of the *stretch* or *neutral* postures, but may occasionally attack out of the fully upright posture (*Rai*) while boxing. Attacks are either followed by retaliation (i.e. an attack on the part of the opponent), which leads to a tumbling ball (*Fgt*: Plate 4), or more commonly a sequence of *chases*, *retreats* (*Ret*), and further *attacks*. Voles very rarely fight for more than a few seconds at a time. Prolonged sequences of *Cha*-*Ret*-*Att* are also very rare. After particularly intense fights, the winner may scent mark in the form of *perineal drags*, *flank scratching*, and *digging* (Skirrow 1969; Skirrow and Ryšan 1976). Active scent marking in *Clethrionomys gapperi* at Heart Lake *only occurs* after intense fights in the neutral arena test situation. When scent marking does occur, it cannot be mistaken for anything but scent marking as described by Skirrow (1969). Nevertheless, it is very rare in the neutral arena trials (Appendix 7), and may not be recorded unless a large number of trials are conducted (e.g. *flank scratching* was not seen in 1975, Mihok 1976). In more natural test situations, scent marking is moderately common, although there appear to be racial differences in its frequency of occurrence in *Clethrionomys gapperi* (Skirrow 1969, McPhee 1977).

Vocalizations are common during encounters and are of two basic types, *squealing* ("Quietschlaute" of Johst 1967) and *teeth grinding* ("Zähnewetzen" of Johst 1967). *Squealing* occurs in many different situations and probably represents at least three different kinds of vocalizations. The common *squeal* (*Voc*) is high-pitched, of short duration, and relatively loud. It typically accompanies Rap or Rai. A squeal usually involves an open mouth display in which the incisors are clearly visible and the lips are somewhat protruded (Voc: Plate 4). This helps to identify the vocalizing animal, and easily distinguishes this vocalization from teeth grinding. When teeth grinding, an animal usually keeps its mouth closed or only partially open, and bares its incisors by drawing back its lips. A much louder squeech (Mihok 1976) is produced from the fully upright position, and is usually repeated many times in short succession. The squeech was often difficult to distinguish from the squeal, and may simply be a particularly intense form of the squeal rather than a separate kind of vocalization. A third vocalization, the squeak, is produced by submissive animals, especially mature males in encounters with mature females. It resembles the squeal in pitch but it is often barely audible, is repeated in quick succession throughout an encounter, and does not involved an open mouth display. The squeak was incorrectly scored as Voc throughout this study, but should definitely be considered a different kind of vocalization in future studies. Teeth grinding is low-pitched and was relatively difficult to hear in this study due to background noises at the Biological Station. It is also common in Microtus (Clarke 1956) and is thought to be mainly produced by animals prior to attacks.

Behaviors that carry no connotation of aggression and are generally thought of as cohesive or "amicable" are relatively common in *Clethrionomys gapperi*, especially among immatures. Animals will sometimes *huddle* (*Hud*), *groom* themselves (*Grm*), or *groom each other* (*Got*) during encounters. *Following* (*Fol*) also occurs during encounters and can often prolong an encounter through a 15-min trial. Prolonged sequences of *Nn*, *Na*, *Hud*, and *Fol* were particularly common among immatures late in the season.

Encounters end with one of three functional actions. Animals either walk away from an encounter (*Withdrawal*: *Wit*) or run/leap away (*Retreat*: *Ret*). Encounters also sometimes end prematurely when a vole distinctly changes direction to avoid contact on approach (*Avoid*: *Avd*).

A summary of the behaviors recorded in detail throughout the study is given in Table 20. A detailed breakdown of the frequency of various behaviors, and the number of trials staged between different kinds of animals is given in Appendix 7 & 8.

Relationships Among Behaviors

Behavior in the neutral arena trials was analyzed in terms of the 22 variables described in Table 20. The behavior of each individual in a trial was quantified by a vector of 22 variables, each of which was coded as the mean frequency of occurrence per encounter after applying a square root transformation (Sokal and Rohlf 1969, page 384). The unit of analysis, the operational taxonomic unit (OTU), was therefore a multivariate description of the behavior of one individual towards another in a trial. The total sample represents 1628 OTU's, i.e. roughly three successful trials per 500 subjects. The OTU's are not classically independent in a statistical sense, since the same individual's behavior is represented more than once in trials against different opponents. Nevertheless, the trials are independent to the extent that behavior is largely situation dependent, i.e. it varies within an individual depending on the nature of the opponent. Preliminary analyses of behavioral data for _Clethrionomys gapperi_ (Mihok 1976) indicated that the relative status of individuals in a trial was of major significance in determining the behaviors that occurred, and I therefore chose to initially analyze behavior without lumping data over a series of trials for one individual.

Relationships among these behaviors are described in terms of correlation coefficients in Table 21. Coding the data in other ways did not appreciably alter the correlation matrix. For example, the correlation matrices produced by coding the data as described, as the raw frequency per trial, or as the binary frequency per trial, were nearly identical (mean cophenetic correlation coefficient = 0.96). A comparison of the correlation matrices generated from the total sample of 1628 OTUs with previous analyses based on only the 1975 (N=141) or the 1976 data (N=726) indicated that correlation coefficients were not inflated by the unnaturally large sample size produced by counting the behavior of each individual in each trial as a separate OTU.

The correlation matrix was further analyzed through various factor analyses (SPSS program FACTOR). Three approaches based on statistically defined factors (Principal Components Analysis), hypothetically inferred factors (Principal Axes Analysis), and psychometrically generalizable factors (Alpha Factor Analysis), yielded similar solutions. For example, the unrotated 7-vector solutions from these analyses had a mean cophenetic correlation coefficient of 0.86. The factor matrix derived from Alpha Factor Analysis was chosen over other analyses for consistency with a previous study (Mihok 1976), and for its intuitively appealing basis in psychometric theory (Cronbach _et al_. 1963; Kaiser and Caffrey 1965). The Quartimax rotated solution from this analysis is given in Table 22, with short identifiers given for each successive factor for future reference. A rotated rather than an unrotated solution was retained for further analysis since the number of unrotated solutions is hypothetically infinite. Factor analysis is a mathematically indeterminate procedure that solves an equation with two unknowns (Z=FP', where Z= original data matrix of standard scores, F= factor score matrix, P'= transposed factor pattern matrix). Rotation provides an optimal set of reference axes that can generally be replicated across studies. Although any rotational strategy can capitalize on chance, rotation usually leads to "simple structure", which results in invariant factors. The degree to which these factors are actually invariant with different methods of analysis can be ascertained from a comparison of the analysis in Table 22 with a Principal Components Analysis of the same data in Appendix 9.

In general, the first four factors (AMI, THR, AGG, SBT) are repeatable regardless of the way in which the data are coded or analyzed. Three data sets were analyzed in the course of this study by various methods (1975, 1976, 1976+1977), and consistently produced factors that could be equated with AMI, THR, AGG, and SBT. The fourth factor (SBT) was relatively underdetermined, as only two variables (Sub, Tur) consistently had salient loadings, and was therefore the most variable across data sets. Plots of eigenvalues against factors (the "scree test") in various analyses indicated that eigenvalues diminish sharply after the extraction of the third factor. The first three factors are therefore repeatable, whereas the fourth and later factors require further confirmation.

The pattern of loadings on the last three factors (AVD, BOX, APV) sometimes varies with different methods of analysis. These factors should therefore be interpreted with caution until other workers have replicated these experiments. In particular, the seventh factor (APV) had only a marginally acceptable eigenvalue (i.e. > 1.0) across most analyses, and was dropped out of the solution in the 1975 data set. In general, either one or two factors representing combinations of approach and avoidance behavior, as well as one factor representing aggressive behavior, are represented among the last few factors in most analyses. These factors require further work, and would particularly benefit from studies that record a larger suite of variables, since they are relatively underdetermined (i.e. few variables have salient loadings). Given these qualifications, the factors derived from the Alpha Factor Analysis have been interpreted as follows:

Repeatable Factors

I. AMI: an amicable factor representing cohesive and contact-investigation behaviors. The pattern of loadings is nearly identical with those of factor I of Mihok (1976) with salient loadings on *Nn*, *Na*, *Hud*, *Got*, *Fol*, and *Wit*. Approach components are represented by high positive loadings on investigation behaviors (*Nn*, *Na*), and a negative loading on a possibly aggressive approach (*Str*). Termination components are represented by high positive loadings on withdrawal (*Wit*), and a negative loading on retreat (*Ret*). Encounter components are represented by tolerance of the other individual (*Hud*), submissive behavior (*Sub*), comfort behaviors (*Grm*, *Got*), and cohesive behavior (*Fol*).

II. THR: a threat factor representing behaviors that are commonly interpreted as either threatening or defensive. The pattern of loadings is similar to that of factor II of Mihok (1976) with salient loadings on *Voc*, *Rap*, *Paw*, *Pw1*, and *Rai*. A major difference from Mihok (1976) is the absence of high loadings on *Str* and *Att*, which is partly due to differences in coding of the data, and partly due to the more reliable sample size for the analysis in this study. Binary coding of the small data set in 1975 obscured some of the underlying relationships between variables, as behaviors occurring in separate encounters were lumped over the entire trial without regard to frequency. As noted in Mihok (1976), retaliation on the part of initially defensive animals accounted for the correlations of defensive and attack behaviors, and hence the overlap in loadings on defensive and attack factors in that analysis.

III. AGG: an attack factor representing purely aggressive behaviors (Att, Cha, Fgt) similar to factor III of Mihok (1976). Rai also has a marginally high loading reflecting a tendency for animals to attack out of both the fully upright posture and the stretch posture. Str has the lowest communality of all the variables, and only weakly loads onto this factor.

IV. SBT: a subordinate factor represented by only two behaviors (Sub, Tur) similar to factor V of Mihok (1976). This factor appears consistently in various analyses although it is underdetermined. A more detailed breakdown of the head-down and turn away postures would possibly define this factor with better accuracy.

Tentative Factors

V. AVD: an avoidance factor marginally comparable with factor IV of Mihok (1976) with high loadings on Hes and Avo. Both of these variables have low communalities, and are therefore relatively unreliable. Nevertheless, they reflect a distinct tendency on the part of some animals to alter their behavior on approach, and may be related to an underlying factor of avoidance.

VI. BOX: a boxing factor similar to factor VI of Mihok (1976) with high loadings on Ret, Fgt, Rai, and Paw. This factor tends to vary slightly in interpretation in different analyses as approach and termination variables sometimes load onto this factor. Nevertheless, there appears to be a consistent factor involving Fgt, Rai, and Paw that is extracted as a possible third component of aggressive behavior in most analyses.

VII. APV: an approach-avoidance factor marginally comparable to factor IV of Mihok (1976) with a salient loading only on Neu, and a marginally high loading on Wit. This factor has a barely acceptable eigenvalue, and is therefore tentatively unreliable. In particular, some analyses result in a six factor solution in which Neu, Hes, Avo, and Wit (and sometimes Ret) load onto a rather general activity factor. Relationships among these approach and termination behaviors require further work with a more detailed emphasis on postures rather than actions.

Although these interpretations are useful in reducing a 22 variable description of behavior to a 7 variable description, some information is lost and some bias is necessarily introduced. In particular, there are no commonly held interpretations of defense, threat, aggression, and a host of other words commonly used to describe behavior (King 1973), and it is hoped that the reader will accept these labels for the factors as descriptive aids rather than rigid definitions.

Reliability

The reliability of each of the original 22 measures of behavior used in this study was not measured and is therefore unknown. Low communalities of many variables suggest that specific variance or error variance is high relative to common variance. Behaviors may therefore have a relatively important unique meaning of their own, or behaviors may be subject to error during the actual test procedure. With virtually no knowledge of the reliability of the variables scored in these trials, it is difficult to differentiate between these two alternatives. The behaviors are simple enough to be easily recognized, and it is therefore unlikely that low communalities reflect misidentification of behavior patterns. Error variance may nevertheless be relatively important since we do not know how captivity and the unnatural test conditions affect behavior. Krebs (1970) has tested the repeatability of a number of rather general behavioral variables in *Microtus*, and has found that repeatability is poor. Repeatability varied between 0.13 and 0.49 for voles retested while held in captivity for a few days, and it varied between 0.09 and 0.73 for voles retested after spending at least six weeks between tests in the field. These repeatability values reflect the repeatability of behavior against different opponents, and therefore tell us little about how the repeatability of behavior is influenced by the nature or the behavior of the opponent. Replicated series of behavioral trials against the same opponents are needed to determine the reliability of behavioral measures currently being used in small mammal studies.

Given these qualifications, I analyzed variability in behavior in terms of the factors derived from the original variables. Factor score estimates (mean=0) were calculated for each factor from the results of the Alpha Factor Analysis. These scores represent a hypothetical measure of the level of amicable, threat, attack, etc. behavior shown by an individual in a trial relative to the sample mean. The accuracy of these scores is only as good as the coefficient of determination between the factor score estimate and the hypothetical factor it represents (Green 1976). Since communalities of many variables were relatively low, some factors were underdetermined, and hence some factor scores were poorly estimated. Scores for AVD, BOX, and APV were poorly correlated with the factors they were supposed to be measuring (Table 22), and must therefore be interpreted with caution. Only the first three factors (AMI, THR, AGG) were estimated well.

Individual variability was estimated from repeated trials of standard voles with numerous opponents in 1977. Coefficients of Variation for factor scores ranged from 45 to 62% for standard males, and from 32 to 52% for standard females. This translates into the fact that a sample size of 30 trials is required to detect a minimum 28% difference in behavior, 90% of the time, at the 5% significance level for the least variable of all the standard voles (Sokal and Rohlf 1969, page 247).

Round-robin encounters at monthly intervals between standard voles indicated that individuals did not change their behavior from May to September (tested by regressing each individual's scores against the day of the trial). Individual males consistently differed in "personality" through the season, whereas individual females did not (Table 23). Differences in the behavior of individual standard males are shown in Fig. 19, with each individual trial represented by a standard stick model in 3-D behavioral space. These four individuals maintained a relatively stable dominance order among themselves through time with 291 > 287 > 282 > 281. In contrast, the behavior of standard females did not show any evidence of "personality" differences, and did not reflect any consistent patterns in dominance. Standard females were extremely nervous and docile, and were almost totally inactive in the neutral arena. Furthermore, I never detected perforate vaginas in these females after their initial capture in early May. This was in spite of the fact that these females were maintained in an animal house in olfactory and auditory contact with numerous other voles.

Trials involving standard females were therefore probably an unreliable indicator of behavior. Future studies should probably allow females to complete at least one pregnancy before isolating them for use as standard opponents.

Individual variation in behavior was also reflected in the poor repeatability of behavior in wild-caught voles paired in three trials with opponents of the same sex, age (OW or YG), and reproductive condition (mature or immature), (Table 24). Correlation coefficients between factor scores of the same individual against three opponents were moderate to poor. In addition, the overall reliability (Cronbach's Alpha) of the 3-trial test was at best moderate by psychological standards (Mehrens and Lehmann 1973). This behavioral variability was not due to accommodation to the test procedure, as factor scores did not differ significantly from the first to the third trials (Analysis of Variance). As a consequence of this lack of repeatability, behavioral scores from neutral arena trials (even with three trials averaged) reflected an individual's behavioral makeup only in a most general way.

Age, Sex and Maturity Patterns

The OTUs were divided into 36 categories based on the sex, age (OW or YG), and sexual maturity (mature or immature) of the individual and the opponent. Patterns in behavior are illustrated in Fig. 20 to 23 for the first four factors, with each histogram representing the mean factor score within any category. Means and standard errors for all factor scores across categories are given in Appendix 10 to 13.

Amicable behavior (AMI) was uniformly common in the behavior of immature females towards all females (Fig. 20). AMI was also common in the behavior of immatures towards young of the year in mixed-sex trials, and in the behavior of immature males towards immature males. Threat behavior (THR) was common in the behavior of immature voles towards overwintered voles in female-female trials (Fig. 21). THR was also common in the behavior of mature females towards overwintered males, and in the behavior of immature males towards overwintered males. Attack behavior (AGG) was common in the behavior of overwintered females towards young females, and in the behavior of overwintered males towards mature males (Fig. 22). AGG was also common in some trials between mature females and certain types of males. Subordinate behavior (SBT) was particularly characteristic of the behavior of mature males towards mature females (Fig. 23). It was also common in the behavior of overwintered animals towards immatures.

These complex patterns across categories and factors were summarized by performing a Q-technique taxonomic analysis of the 36 OTU categories. The seven mean factor scores in each category were used to calculate a dissimilarity matrix of squared Euclidean distances between categories; this matrix was then analyzed by UPGMA cluster analysis (Fig. 24). Profiles for each cluster are given in

Table 25, with a summary of behavioral strategies in Table 26.

Sample sizes for some of the strategies in Table 26 were small (Appendix 8), especially for most immature-mature trials, and some male-female trials. In male-female trials, maturity was the main factor determining behavior. Mature males typically emphasized subordinate behavior (SBT) in trials with mature females, which in turn emphasized either threat (THR) or attack (AGG) behavior. If either of the animals in mixed-sex trials was immature, behavior was generally amicable.

Within-sex trials differed considerably between males and females. Overwintered males behaved aggressively towards *mature* males, whereas overwintered females behaved aggressively towards *young* females. Mature young of both sexes did not emphasize any particular strategy of behavior. Immature young behaved amicably towards other immatures, but behaved in different ways towards other animals. In particular, immature males emphasized threat behavior towards overwintered males, which in turn behaved submissively. One unexpected finding was the lack of any particular strategy in trials between overwintered females.

Behavioral Hierarchy

A composite index of overall dominance was calculated for each trial between the behavior of an individual and its opponent to determine the relative status of sex, age and maturity categories in the population:

Dominance= dAGG + dTHR + dBOX - dSBT - dAVD - dAPV. From this definition, the animal with the higher scores on the attack, threat and boxing factors, and the lower scores on the subordinate, avoidance and approach-avoidance factors, is defined as the dominant animal $(D > 0)$. This analysis indicated that there was a distinct linear hierarchy within the population (Table 27), although only 3 of 15 individual comparisons were significant. The dominance order from top to bottom was: overwintered females, young mature females, young immature males, young immature females, overwintered males, and young mature males.

Temporal Variation

Behavior observed at any specific time was highly variable due to the changing composition of the population and the variable emphasis of behavior in encounters between different kinds of animals. Comparisons between different times are therefore only valid within categories, since virtually any average behavioral score can be generated by pairing only certain kinds of animals. For example, consider the path of female-female behavior through time in 1976 and 1977 (Fig. 25). The large seasonal and yearly differences in behavior were a function of both subtle changes in behavior within some categories (Table 28), and seasonal trends in demography which changed the nature of the participants through time. Through most of 1976, behavior was generally aggressive as numerous young were captured and much of the sample consisted of trials between overwintered females and young of the year. By period 6 of 1976, most of the overwintered females had died and the population was mainly composed of immatures, resulting in a dramatic swing to more amicable behavior. In 1977, there was a general shift to more amicable behavior in overwintered females (Table 29), which in combination with poor recruitment produced relatively amicable average scores early in the season. Aggressive behavior was only common in period 4 when young were first caught in any numbers, and numerous trials between overwintered and young voles were staged. A further shift towards more amicable and less aggressive behavior occurred in periods 5 and 6 as more immatures and fewer overwintered animals were captured.

Behavioral variation between 1976 and 1977 within categories of the OTUs is summarized in Fig. 26 & 27, with statistics given in Table 28 & 29 for groups with acceptable sample sizes. Note in particular that sample sizes for some of the points in Fig. 26 & 27 are relatively small (Appendix 8), and that some categories are not shown due to extremely small sample sizes. In female-female trials, there were a number of significant differences between years, reflecting a possible general trend towards more amicable behavior in 1977 (Fig. 26). This shift was highly significant only in overwintered females (Table 28 & 29). In male-male trials (Fig. 27), only the behavior of immatures appeared to differ significantly between years (Table 28). This shift in behavior was mainly due to lower levels of attack (AGG) and subordinate (SBT) behavior in 1977 (Table 29). In general, year differences in behavior were subtle, and there was no evidence for consistent or widespread changes in behavior throughout the population.

Predictability of Behavior

The relationships between behavior in the neutral arena trials and certain variables were tested for groups with moderately large sample sizes (OW F vs OW F, OW M vs OW M, Y- M vs Y- M). Within each category, a stepwise multiple regression was performed between factor scores and the dominance index, and the following variables:

(1) year of the trial,

(2) day of the trial,

(3) "potential" familiarity (caught on same or different traplines),

(4) molar root length or M^2 age estimate,

(5) corrected weight,

(6) body length,

(7) rank of capture (caught on 1st, 2nd, etc. trap check),

(8) days from capture to trial.

Results of multiple regressions using these predictor variables were poor, and did not reflect any consistent trends across groups (Appendix 14).

The relative status of individuals in a trial was also analyzed by comparing winners (Dominance Index > 0) and losers (Index < 0) within categories of the OTUs.

Comparisons were made between the individual and its opponent in a trial for the following variables:

(1) Age (older in overwintered animals if molar roots longer, older in young if root category greater, roots formed > groove closed > groove open),

(2) Light wounding (has more wounds if has at least 5 more light wounds),

(3) Severe wounding (has more wounds if has at least 1 more severe wound),

(4) Rank of capture (greater if caught later in the sequence of trap checks),

(5) Weight (heavier if at least 1 g heavier),

(6) Length (longer if at least 5 mm longer).

Only animals autopsied within 5 days of the trial were used for weight and length comparisons.

In trials between mature females, winners were longer than losers ($X^2=13.1$, $P < 0.001$). This trend was also evident when animals of the same age-class were lumped (OW vs OW and Y+ vs Y+, $X^2=5.3$, $P < 0.025$), suggesting that the dominance of overwintered females over young mature females (Table 27) was partly size-related. All other comparisons in female-female trials were not significant. In male-male trials, the only significant trend was a tendency for winners to be shorter in immature-immature trials ($X^2=6.3$, $P < 0.025$). Comparisons of winners and losers were also made separately for trials in which the opponents were caught on the same or different traplines. Obvious winners (Dominance

Index > mean Index) and obvious losers (Index < - mean Index) were also compared. Trends in these two comparisons were the same as in the original comparisons of winners and losers. In general, age, wounding, rank of capture, and size variables were poor predictors of dominance within population categories. Dominance appeared to be mainly a function of the hierarchical population structure based on sex, sexual maturity, and age-class (Table 27).

The overall status of individuals in behavioral trials was analyzed by comparing animals that won (Dominance Index > 0) zero, one, two, or three trials in the round-robin sequence. Only animals paired with voles of the same sex, age-class, and sexual maturity were included in this analysis (N=141). X^2 or F tests on weight, length, transferrin phenotype, light wounding, severe wounding, rank of capture, litter size, and age in these four groups were calculated for each sex and each age-class separately. The only significant trend was found in body length for overwintered females (F=3.37, df=3,35, P=0.03). Overwintered females that won one, two or three trials averaged 12 mm longer than overwintered females that won no trials (Duncan's Multiple Range Test). The number of animals winning 0, 1, 2, and 3 trials was also compared between years, sexes, and age-classes to see if dominance was more clearly expressed in any of these groups. None of the X^2 tests was significant.

The habitat where animals were caught was also used as a possible set of variables for the discrimination of winners from losers. For this analysis only two groups were recognized, winners (winning 2 or 3 trials), and losers (winning 0 or 1 trial). A Discriminant Functions Analysis of habitat variables with sufficient variation between winning and losing groups was significant (Table 30). The pattern of coefficients suggests that winners came from *Picea glauca* moss forests with tall deciduous shrubs (Map unit 2 of Talbot 1978), and losers came from lichen woodlands with low deciduous shrubs (Map units 14 & 17 of Talbot 1978). Coefficients for ground moisture and *Ledum groenlandicum* suggest that losers may also have come from bog habitats, although these were not sampled extensively.

Habitat preferences on the multiple capture grid only partially reflected the trends in Table 30, mainly due to the small number of habitats sampled by the grid. Significant habitat variables were selected by performing a stepwise multiple regression analysis of the number of captures at each trap station in 1977 with the habitat scores at each trap station. Capture frequencies were positively related to high densities of *Alnus crispa* and graminoids & sedges, and were negatively related to high densities of *Picea glauca* and lichens (Table 31). These trends reflected the low frequency of captures in a dense stand of pure *Picea glauca* and in scattered stands of *Pinus banksiana* woodland (Table 32). High capture frequencies occurred in areas of mixed *Picea glauca* - *Pinus banksiana* forest, especially in dense stands of *Alnus crispa*. The areas preferred by *Clethrionomys gapperi* on the multiple capture grid appear to roughly correspond to the habitat in which winners were caught (Table 30).

Variation with Pregnancy

Since females were allowed to litter in captivity, their reproductive status at the time of the behavioral trials could be determined accurately. An analysis of behavioral differences between quiescent, pregnant, and lactating females is given in Table 33. Among the more reliable factors, differences in attack behavior (AGG) were significant, with an increase in this behavior from quiescent to pregnant to lactating females. In pregnant females giving birth to their first litter, there was significant heterogeneity in scores on AGG depending on the number of days tc parturition (lumping over 2 day intervals, F=3.56, df=11,62, P=0.006). This was related to a general trend for an increase in attack behavior in pregnant females about one week befcre parturition (Fig. 28).

Behavior and Fitness

Due to the relatively low population densities in 1977, sample sizes for the behavior of wild-caught voles from the behavioral grid were very small. Consequently, behavior of these voles had to be compared with estimates of survival and home range size in a most general way, lumping all animals (male and female). Mean factor scores of individuals against four standard opponents were compared for animals that survived to the next sampling period and for animals that did not survive (Table 34). Survivors had significantly higher scores on the threat factor (THR) than non-survivors. Mean factor scores were also compared in animals with home ranges larger or smaller than the population mean (Table 34). None of these comparisons was significant.

Five photographic sessions were specifically staged between four mature males and a potentially estrous female in 1977. Two of these sessions resulted in matings by the male I had scored as dominant in the neutral arena trials the previous evening (P=0.06). In these two sessions, the dominant male fought with the other three males initially and restricted them to the periphery of the photographic arena. The dominant male subsequently spent most of its time with the female while the other males avoided contact with either the dominant male or the female. After about 15-min of repeated bouts of chasing and following (Christiansen and Døving 1976), the female became receptive and the male copulated with her repeatedly over the next 10 min. At no time did any of the other males attempt to interfere with mating between the dominant male and the female.

Summary

1. Interactions between immatures were amicable.
2. Mature males behaved submissively towards mature females, which threatened or attacked the males.
3. Attacks and fights mainly occurred between overwintered females and young of the year, and between overwintered males and mature males.
4. The population dominance hierarchy from top to bottom was: overwintered females, young mature females, young immature males, young immature females, overwintered males, young mature males.
5. Female-female interactions were more amicable in 1977; other types of interactions did not vary appreciably between years.
6. Few variables were consistently related to behavior or the level of dominance in neutral arena trials. Size (body length and not body weight) was the only consistent indicator of dominance in female-female trials.
7. Animals that won in trials against similar opponents came from different habitats than animals that lost. This appeared to reflect an association between winners and the preferred habitat of *C. gapperi*, *Picea glauca* moss forests with an understory of *Alnus crispa*.
8. Animals that survived to the next sampling period on the behavioral grid had higher scores on the threat factor (THR) than animals that did not survive.

DISCUSSION

Demography

In 1974, Krebs and Myers reviewed the demography of microtines and challenged researchers to find populations that do not cycle. Since 1974, researchers have reported non-cycling populations of *Clethrionomys rutilus* (Martell 1975; Whitney 1976), *Microtus breweri* (Tamarin 1977), *M. pennsylvanicus* and *M. ochrogaster* (Birney *et al*. 1976), *M. agrestis* (Rasmuson *et al*. 1977; Hansson 1978), and *Synaptomys cooperi* (Gaines *et al*. 1977). Other studies have similarly shown that cycles do not always conform to the "normal" pattern (LeDuc and Krebs 1975; Krebs *et al*. 1976; Gaines and Rose 1976). Gaines and Rose (1976) concluded that a realistic interpretation of the demography of microtines is one of a continuum of annual and superannual fluctuations in density. Population cycles are obviously more variable than has previously been assumed (Gaines *et al*. 1977), and there are as yet no convincing arguments for why a species or a population does or does not cycle. Hypotheses advanced to explain the absence of superannual cycles include: suboptimal habitat (Koshkina and Korotkov 1975; Martell 1975), narrow niche breadth (Whitney 1976), low vegetative cover (Birney *et al*. 1976), and lack of a dispersal sink (Tamarin 1978).

Clethrionomys gapperi at Heart Lake probably falls near the middle of the continuum between annual and superannual fluctuations. Most years are characterized by relatively low spring densities with a modest increase during the breeding season (Fig. 16). Years of exceptional increase (1961, 1962, 1974, 1976) are rare, as are years of very low density (1964, 1965). Peaks in density occur at roughly 4-year intervals (1962, 1966, 1970, 1974, 1976), but are weakly expressed relative to large annual changes in density. High densities only occur in the fall, and have probably never exceeded 12 animals / hectare in 18 years of research (Fuller 1977a). In contrast, southern populations of _C. gapperi_ have reached densities as high as 35/ha (Merritt 1976, my estimate), and 40/ha (Miller and Getz 1977). Similarly, species of _Microtus_ that show more typical superannual cycles have peaked at densities ranging from 100/ha (Krebs _et al_. 1969) to 1300/ha (Boonstra and Krebs 1978).

Although absolute densities at Heart Lake are low in comparison with other populations, rates of increase and decrease are comparable. Population growth in 1976, when expressed as the instantaneous rate of increase in numbers per week (r=0.098), fits into the top 25% of the range of growth rates measured in 38 increasing populations of microtines (Krebs and Myers 1974, Table 3). Similarly, the decline in numbers from the fall of 1976 to the fall of 1977 is comparable with the typical decline seen in most population cycles (Type H: a decline with recovery during the breeding season, Chitty 1955). This decline was initially the result of poor winter survival, followed by poor juvenile survival during the breeding season. Other researchers have observed winter declines in *Clethrionomys* in a variety of species and localities (Crawley 1969; Fuller *et al*. 1969; Jensen 1975; Whitney 1976; Fuller 1977a; West 1977; Kucera and Fuller 1978; Merritt and Merritt 1978a), but have failed to identify the causes of poor winter survival. Numbers typically drop gradually from one fall to the next spring, but may occasionally remain high through winter and then drop sharply in early-spring. Poor survival in early-spring is sometimes associated with adverse environmental conditions (Whitney 1976; Merritt and Merritt 1978a), and may therefore be unrelated to regulatory features in populations. Since I did nct trap during winter, I have no explanation for the severity of the winter decline in 1976-77. If animals compete for favorable overwintering microhabitats (West 1977), then the variation in winter survival seen on the multiple capture grid may simply be an artifact of the number of suitable overwintering sites in a particular winter. The relatively constant spring densities seen throughout this study suggest this possibility. This hypothesis could be tested by monitoring environmental conditions on live-trapping grids through winter. Occupancy of favorable microhabitats should improve the survival of certain individuals. Since levels of aggression, and hence competition, appear to be low in winter (Ivankina 1977; West 1977), competition and differential survival may only become significant at the start of breeding just prior to snow-melt.

Poor juvenile survival was the second main factor responsible for the decline in numbers following the peak in 1976. Since juveniles were rarely captured, I have no information concerning the reasons for poor survival. In common with other studies, survival of young voles raised from birth in captivity in 1977 was good, even though animals were dying in the field. Adjusted juvenile survival rates in this study (28% to 76%) were comparable with estimates of juvenile survival in other species of *Clethrionomys* (*C. glareolus*: 47-61% (Ryszkowski and Truszkowski 1970), 29-66% (Petrusewicz *et al.* 1971), 32-52% (Bujalska 1975); *C. rutilus*: 27-60% (Whitney 1976); *C. rufocanus*: 8-89% (Viitala 1977)). This variation in juvenile survival is often the main factor contributing to cyclic density variations (Krebs and Myers 1974), but has not been extensively studied. In *Microtus*, recent work on the manipulation of sex ratios has shown that social structure (Redfield *et al.* 1978a), and the density of adult females (Boonstra 1977, 1978; Redfield *et al.* 1978b) may affect juvenile survival. Neither of these factors varied between years of markedly different juvenile survival in this study. Poor juvenile survival has also been related to low May-June environmental temperatures (Okulova 1975) and extensive snow melt-off in spring (Whitney 1976). Poor juvenile survival in 1977 was correlated with an unusually cold summer. Similarly, good juvenile survival in 1976 was correlated with particularly warm temperatures late in the season (Fuller, unpublished). Trends in juvenile survival may therefore reflect environmental differences between years as well as qualitative differences in animals from separate phases of the population cycle (Fuller 1977b).

Reproduction, survival, and growth did not differ appreciably between peak and decline years in this study. This is not typical of a cyclic microtine. Krebs and Myers (1974) found that a longer breeding season, and a lower age (weight) at sexual maturity were common features of increasing populations. They also felt that poor adult survival overall, and poor survival in males in particular, were common features of declining populations. Lastly, high growth rates and large body size are supposedly associated with increasing populations. I found no evidence for any of these trends in all the demographic data collected from general trapping, multiple capture trapping or animals raised in captivity. Various European workers have also claimed that the proportion of mid-summer young maturing in the year of their birth is inversely related to spring (overwintered) densities (Kalela 1957; Bujalska 1970, 1973; Koshkina and Korotkov 1975; Viitala 1977). Trends from the multiple capture grid did not support this hypothesis. Furthermore, animals raised in captivity appeared to mature as a function of season, with only a very minor proportion of animals maturing or not maturing in a short time-span in the middle of the season. The absence of this regulatory feature in *C. gapperi* at Heart Lake appears to be related to the relatively suboptimal conditions found at Heart Lake, which result in a short breeding season, and relatively low population densities. For example, Koshkina and Korotkov (1975) have found that populations of *C. rutilus* living in suboptimal habitats do not show any evidence for the self-regulation of population density through the inhibition of sexual maturity. In populations where the inhibition of sexual maturity is indisputable (e.g. nearly 100% in all young of the year), spring snap-trap indices were about 10 voles per 100 trap nights (TN) in *C. rufocanus* (Kalela 1957), and 20/100TN in *C. rutilus* (Koshkina and Korotkov 1975). In comparison, spring densities of *C. gapperi* at Heart Lake average 1-3/100TN, and have not exceeded 6/100TN. Similarly, spring densities in unregulated populations of *C. rutilus* are 2-8/100TN (Koshkina and Korotkov 1975), and 1/100TN (Martell 1975). Further clarification of these trends requires data from southern populations of *C. gapperi* that exist at much higher densities.

Sex ratios in *C. gapperi* were typically male-biased rather than female-biased as in *Microtus* (Myers and Krebs 1971a; Myllymäki 1977b; Hansson 1978), and did not conform to variations expected on the basis of density fluctuations (Kalela 1971; Hansson 1978; Hansson *et al.* 1978). In common with other microtines, there was a surplus of males in the subadult component, and a surplus of females in the adult component of the population. These trends were nevertheless independent of density variation between 1976 and 1977. For example, Kalela (1971) and Hansson (1978) have suggested that these skewed sex ratios are a feature of peak populations only, and occur as a result of differential sexual maturity. Lack of cyclic changes in sex ratios has been interpreted as one of the symptoms of a non-cycling population in studies of different populations of *M. agrestis* in Sweden (Hansson 1978). These ideas are consistent with some of the data on microtines, but fail to account for the overall male-biased sex ratios in some populations that definitely cycle (Hansson 1978; Hansson *et al*. 1978). Whether these male-biased sex ratios are due to differential trappability, growth, dispersal, movements, or mortality is impossible to say with the present data (Myers and Krebs 1971a). Weights, survival rates, trappability, and home range sizes of immature *C. gapperi* caught on the multiple capture grid were all relatively comparable in males and females, suggesting that differential mortality prior to first capture or differential dispersal was responsible for skewed sex ratios. Since estimates of juvenile survival exceeded 100% in 1976, differential dispersal may be the more likely explanation. The multiple capture grid probably sampled a variable number of possible transients in each year (animals caught only once). If males dispersed more than females, especially in the peak year (Krebs and Myers 1974), then one would expect to record a consistent bias towards males in grid trapping. Male-biased dispersal is common in *Peromyscus* (Stickel 1968; Fairbairn 1978a), and in some (Krebs *et al*. 1976; Myllymäki 1977b), but not all studies of *Microtus* (Myers and Krebs 1971b; Tamarin 1977). It has nevertheless not been adequately demonstrated in *Clethrionomys* (Smyth 1968; Watts 1970b; Koshkina *et al*. 1972; Mazurkiewicz and Rajska 1975; Kozakiewicz 1976), except in one study (Bol'shakov *et al*. 1973). Further research on *Clethrionomys* would benefit from nest box studies in conjunction with radioactive tagging (Hilborn and Krebs 1976).

Behavior

Observations of the behavior of primarily nocturnal, cryptic rodents under natural conditions are very rare in the literature, and have generally been unsuccessful in contributing more than anecdotal observations on the lives of these animals (Andrzejewski and Olsewski 1963; Kikkawa 1964; Clough 1968; Skirrow 1969; Petrov and Mironov 1972; Garson 1975). Researchers have typically relied on indirect methods of observation to assess behavior. Commonly used methods include the analysis of patterns in multiple captures (Burt 1940; Getz 1972; Rajska-Jurgiel 1976), spatial distributions (Batzli 1968; Metzgar 1971, 1979), wounding indices (Christian 1971; Rose and Gaines 1976; Rose 1979), and neutral arena behavioral tests (Krebs 1970; Turner and Iverson 1973; Conley 1976; Fairbairn 1978b). Detailed observations of animals in enclosures (Skirrow 1969; Friesen 1972; Ambrose 1973; Myllymäki 1977a, 1977b), and radiotelemetry studies (Banks et al. 1975; Madison 1977, 1978; Jannett 1978) have also been used. In this study, I chose to monitor behavior in three different ways, multiple capture trapping, wounding indices, and neutral arena behavioral tests, each of which yields qualitatively different information on various aspects of behavior.

Multiple capture trapping generates information on the spatial organization of a population, i.e. it records the pattern and frequency of contacts. For a multiple capture to occur, two animals must visit the same location in a 12-hr period, and one of them must be willing to enter an occupied trap. A multiple capture therefore reflects both spatial proximity and behavioral tolerance. These two factors are presumably interrelated, and cannot be separated without direct observation. The extent to which established behavioral and genetic relations within a population affect the pattern of multiple captures is a particularly critical problem and requires further work. To date, most workers have taken the common sense interpretation that a multiple capture represents an amicable, tolerant or neutral meeting between animals (Burt 1940; Getz 1961, 1972; Rajska-Jurgiel 1976). This interpretation is based on the infrequency of wounding in multiple captures and the generally good survival of animals involved in multiple captures. Data from this study support this interpretation in general, as striking differences in the frequency of multiple captures in mature and immature individuals were correlated with similar differences in levels of wounding and in the extent of amicable behavior shown in the neutral arena trials. Direct confirmation of the "amicable" interpretation has nevertheless not been shown experimentally, and would benefit from experiments similar to those of Taylor (1976). This is particularly critical, since one worker (Viitala 1977) has reported some wounding in multiple captures.

Patterns of association on the multiple capture grid reflected numerous aspects of the social structure of *C. gapperi* in the field. Social structure in mammals has generally been described in terms of three strategies: mating, rearing, grouping and dispersion (Crook *et al*. 1976). The mating strategy of *C. gapperi* appears to be a promiscuous one with numerous associations of brief duration between mature males and females. This conclusion is supported by the infrequency of multiple captures in mature voles, and the general lack of repeat captures of the same individuals. Interactions in the neutral arena similarly reflected little amicable behavior on the part of mature individuals, even in male-female trials. Similar random associations in multiple captures have also been observed in *M. pennsylvanicus* (Getz 1972). Pearson (1960) found some evidence for familial associations in *M. californicus*, but these were generally short-lived. Other workers on microtines (Koshkina *et al*. 1972; Myllymäki 1977a; Viitala 1977) have also typically inferred promiscuity from the large home ranges of mature males in live-trapping studies.

In contrast, other small rodents may form strong male-female bonds (Howard 1949; Blair 1951), or weak bonds (Terman 1961; Davenport 1964), within either polyandrous systems (Myton 1974) or polygynous systems (Brown 1969).

Rearing strategies in C. gapperi appear to reflect the same lack of association seen in mating strategies. The infrequency of multiple captures of mature males with mature females suggests that the male is not a member of the rearing group. Pearson (1960) observed family groups of M. californicus, and similarly found no correlation between the movements of lactating females and juveniles, and the movements of adult males. The duration of the mother-infant bond in C. gapperi appears to be relatively short, and probably ends at weaning. This conclusion is based on the infrequency of multiple captures of mature females with immature voles. Although I have long capture records for a number of mature females, I rarely caught them with immatures until late in the season, towards the end of breeding. Immatures also appeared to settle into the interstices between female territories, and did not remain within what may have been their natal ranges. This contrasts with trends seen in Microtus, where extended families consisting of mature females and their immature offspring may form (Frank 1957; Myllymäki 1977a; Jannett 1978). The only evidence I have for this phenomenon is a few multiple captures of mature females with immatures late in the season, which possibly reflect an association between a female and her last litter. This lack of association in *C. gapperi* was not an artifact of multiple capture trapping, since *Peromyscus maniculatus* inhabiting the grid were caught in large groups that appeared to be extended families (Mihok 1979).

Grouping and dispersion strategies were described in terms of group size, group stability, refuge utilization, and range exclusivity by Crook *et al*. (1976). Taxonomic analyses of group structure through the use of multiple capture data indicated that "groups" in *C. gapperi* existed only to the extent that an animal was likely to come into contact with its nearest neighbors. There were no clearly defined subdivisions to the population. Group size and stability were therefore related to population density and turnover rates, rather than to an ordered set of social rules. This contrasts with the dispersion system of *Microtus*, which may be centered on unstable family groups of about six individuals that occupy specific runway systems and have little contact with other groups (Pearson 1960). This lack of structure in *C. gapperi* has an extremely important consequence in terms of the frequency of behavioral contacts in a population. Contacts increase with increasing density in *C. gapperi*, whereas contacts probably do not increase in *Microtus* (Pearson 1960; Carrol and Getz 1976). Other circumstantial evidence for group structure in microtines is extensive, but is almost entirely based on home range overlap. Various studies have reported promiscuous groups (Viitala 1977), extended families (Frank 1957; Myllymäki 1977a; Viitala 1977), and polygynous groups (Myllymäki 1977a; Viitala 1977). The diversity of systems observed in *Microtus* has been related to female territoriality (Getz 1961; Madison 1978), which may vary with population density (Jannett 1978), and habitat stability (Viitala 1977). Standardized and replicated studies on populations of *Microtus* are sorely needed to explore the diversity of group structures inferred from trapping studies.

The situation in *Clethrionomys* is somewhat clearer, although most studies have also only analyzed spatial distributions on live-trapping grids. A relatively universal feature of *Clethrionomys* spp. appears to be female territoriality, which has been observed in a large number of studies (Kalela 1957; Bujalska 1970; Friesen 1972; Koshkina *et al*. 1972; Imaizumi and Imaizumi 1976; Wells 1976; Viitala 1977; and others). Multiple captures of *C. gapperi* in this study, and "pseudo" multiple captures of *C. glareolus* in Poland (Rajska-Jurgiel 1976) have also clearly demonstrated a strong spatial avoidance between mature females. In contrast, mature males overlap extensively within very large home ranges (Wells 1976). Some researchers have also claimed that mature males of *C. rufocanus* and *C. rutilus* associate in "clans" in which dominance-subordinance relationships exist (Kalela 1957; Koshkina *et al*. 1972; Viitala 1977). This conclusion does not appear to be justified for *C.*

gapperi considering the infrequency of multiple captures of mature males. Mature male home ranges do overlap extensively, but males probably avoid each other within these extensively overlapping ranges. Space appears to be partitioned on a much finer scale in males than in females, and probably involves a short-term occupation of a relatively small area within a large home range. This is presumably related to competition by mature males for females, which requires continual movement over a wide area, as opposed to competition by females for resources to raise litters, which requires an exclusive foraging area (Boonstra 1977). I therefore believe that previous workers on *Clethrionomys* have mistaken male home range overlap as evidence for group structure, when it simply reflects a male's attempts to keep in contact with a number of territorial females that may come into estrus at any time. Male ranges may therefore appear to be clustered or grouped (Koshkina *et al*. 1972) in areas of high female density, even though no actual social grouping exists.

Observations of behavior in the neutral arena trials complemented data from the multiple capture grid on the frequency and pattern of contacts by providing information on the type of contacts between different segments of the population. Previous workers have largely concentrated on interspecific behavior in *C. gapperi* (Getz 1969; Grant 1970; Murie and Dickinson 1973; Turner *et al*. 1975; McElman and Morris 1977; McPhee 1977), and as a result little is known about intraspecific behavior (Skirrow 1969; Mihok 1976). Detailed behavioral studies that go beyond the simple description of behavior in wild rodents are also very rare, with only a few quantitative studies to date (Krebs 1970; Turner and Iverson 1973; Conley 1976; Garten 1976, 1977; Fairbairn 1978b). Furthermore, no one has attempted to describe intraspecific behavior in the population as a whole. In particular, there has been a historical bias towards only observing the behavior of adult males in microtines, a bias that appears to date back to earlier studies on aggression in *Mus* and *Peromysucs* (Archer 1970). This bias has been a considerable red herring for a number of years, particularly in North American studies, and is only now being eliminated. Recent studies have shown that females play a critical role in the restriction of recruitment in *M. townsendii* (Redfield *et al*. 1978b), whereas males play an insignificant role (Krebs *et al*. 1977). This has led to current experiments on the behavior of females as well as males (Krebs *et al*. 1978).

Behavioral patterns observed in *C. gapperi* in the neutral arena were generally comparable with those described for European species of *Clethrionomys* (Johst 1967). Active scent marking behavior was rare in the trials, probably due to the unnatural substrate (wood shavings) used in the trials, and the "neutral" rather than "home" environment the animals were observed in. The extent to which animals scent mark in the field is unknown, athough they obviously scent mark under semi-natural conditions in enclosures (Skirrow 1969; McPhee 1977). Some form of communication, besides actual aggression, is presumably involved in the maintenance of female territories (Viitala 1977), since overwintered females in particular do not fight to a great extent with other overwintered females in the neutral arena. Secretions from the flank and perineal glands (Quay 1968; Skirrow 1969), and urine (Johnson 1975) are three of the known sources of chemical communication in Clethrionomys. Chemical communication in microtines has been implicated in the advertisement of territories (Skirrow 1969), the recognition of sex and individuality (Wilson 1973), and the recognition of social status (Stoddart et al. 1977). Behavioral differences in animals exposed to familiar and unfamiliar individuals have been shown in field populations (Ivankina 1974), as have differences associated with the recognition of local populations (Godfrey 1958).

Female-female behavior in the neutral arena indicated that aggression was common mainly in the behavior of overwintered females towards young of the year. This observation suggests that female behavior is critical in limiting recruitment into the population. Aggressive interactions presumably prevent young females from settling into occupied areas, a trend that was obvious for mature young, and to a lesser extent for immature young on the muliple capture grid. Spring densities of C. gapperi at Heart Lake are relatively low in most years, and it is therefore unlikely that unoccupied space is sufficiently scarce for an actual "floating" population (Krebs et al. 1978) to form. Since young animals (< 30 days) were rarely captured, it is not clear whether juvenile mortality is at least partly related to aggressive interactions with overwintered females. Numbers of young mature females born into the population during the relatively short maturation period at Heart Lake are probably insufficient in most years to fill up all of the available space even in years of good juvenile survival. Behavioral interactions resulting from competition for space may only be significant in determining the fate of recruits later in the season, when voles attempt to settle into areas that are already completely occupied by mature females. Behavioral differences between animals caught in different habitats suggest that a "floating" population of "losers" may exist in certain habitats. If these habitats are suboptimal, then competition for space may still be important even though spring breeding densities are low and space appears to be plentiful (e.g. overwintered animals may exclusively occupy all of the available optimal habitat in spring, leaving only suboptimal habitat unoccupied). This phenomenon is thought to be characteristic of rodent populations (Anderson 1970), but has only been demonstrated in one study to date (Krebs et al. 1978). The patchiness and diversity of habitats at Heart Lake (Talbot 1978) provides an excellent framework for this type of process, but this hypothesis would be difficult to test given the low densities and behavioral variability of _C. gapperi_. Restricted recruitment may only occur in peak years such as 1974 and 1976, when either overwintered densities or juvenile survival is particularly high. Experiments on the introduction and removal of successive cohorts of young into field populations (Healey 1967; Boonstra 1978) would help to determine the forces that limit recruitment in _Clethrionomys_ populations.

Male-male behavior in the neutral arena indicated that aggression is particularly common in encounters between mature males. Mature males appear to compete for the insemination of females on an opportunistic basis since they do not associate with any particular female, and do not occupy an area exclusive of other males. Aggression may therefore improve the fitness of a mature male if it acts to reduce the number of mature males in a male's general area. The female-biased sex ratios in mature young imply that either dispersal of subordinate males or inhibition of sexual maturity in males (Viitala 1977, and others) are the two main forces acting to reduce the number of mature males in competition with overwintered males for females. Actual behavioral interactions responsible for these two hypothetical processes have not been observed in any _Clethrioromys_ population, although both processes appear to be plausible from data on live-trapped populations. Aggression may also be important during actual mating in _Clethrionomys_. Kalela (1957), Koshkina _et al_. (1972), and

Viitala (1977) have described "estrous" runs in which females travel outside of their normal ranges. Kalela (1957) has also described chase and copulation sequences between a mature female and more than one mature male during estrous runs. Intense aggression between mature males may occur during these estrous runs when aggression has a definite payoff in fitness to the males. This may explain why defensive and threat behaviors are commonly observed when animals meet in the field (Clough 1968), rather than attack and fighting behaviors.

Besides the relationship between behavior and recruitment in females, and behavior and fitness in males, there appears to be an overall pattern to behavior, which is related to the demographic profile of C. gapperi. Voles at Heart Lake produce in total about 30 young through the breeding season per individual overwintered female present in spring. This level of reproduction appears to be representative of the maximum output found in many Clethrionomys populations (Okulova 1975), and contrasts sharply with the output of "regulated" populations (roughly four young in C. rutilus). This maximal reproductive effort is related to a dominance hierarchy, which favors individuals that contribute most to an increase in numbers. Mature females are naturally first in the hierarchy, since they contribute directly to an immediate increase in numbers. Similarly, overwintered females are dominant over young of the year females since they produce larger litters.

Immatures occupy a middle position in the hierarchy, presumably because they represent the reproductive component of the population in the following year. Mature males occupy a low position in the hierarchy since they are common enough to insure that all females are mated (Krebs and Myers 1974). This ordering of the population coincides nicely with the demographic strategy of subarctic _C. gapperi_, but obviously needs to be tested on other populations. Populations in more benign environments should not have the same social structure if this hierarchy has in fact evolved as an adaptation to subarctic conditions.

Behavioral contacts in a population can only be analyzed indirectly through grid trapping and neutral arena behavioral tests. Different methods may produce different results, and since we do not know what animals actually do in the field, we have no absolute yardstick with which to measure the biases in our techniques. Of all the indirect methods of assessing behavior, wounding indices are possibly the most intuitively appealing. They are presumably an accurate measure of the actual number and intensity of fights that occur in the field. Wounding nevertheless has its own hidden bias, since it is a highly selective record of fighting only, which appears to be a very minor component of the behavioral interactions occurring in field populations (Andrzejewski and Olszewski 1963; Clough 1968). Given the infrequency of fighting in neutral arena trials of _C. gapperi_, it is especially difficult to equate behavior in the arena with levels of wounding. The situations in which fights and wounding occur in the wild are still largely unknown. Intense aggression has been observed only in the behavior of females around the time of parturition in enclosure studies (Skirrow 1969; Friesen 1972).

Major trends in wounding in *C. gapperi* were related to sexual maturity and year differences. Immatures had consistently low levels of wounding, in agreement with Christian (1971), but contrary to the results of Rose and Gaines (1976) and Rose (1979). In particular, both of these authors have found moderate levels of wounding in immature males of *M. ochrogaster* and *M. pennsylvanicus*. Males in general have more wounds than females in *Microtus* (Christian 1971; Turner and Iverson 1973; Rose and Gaines 1976; Krebs *et al*. 1978; Rose 1979), but females may still have substantially high levels of wounding (Lidicker 1973; Rose 1979). Sex differences in the amount of wounding in mature animals do not appear to be as pronounced in *Clethrionomys* (Martell 1975; Dickinson 1976; McPhee 1977), presumably due to similar levels of aggression in the sexes (Mihok 1976). At present, there are no studies on the behavior of female *Microtus* for comparison.

Differences in wounding in mature voles between years were clearly related to changes in population density rather than changes in behavior. Levels of wounding were highest in mid-summer when mature young were recruiting into the population, and numerous aggressive interactions between overwintered and young mature voles were presumably taking place. Wounding therefore reflected differences in the number of contacts with other individuals rather than behavioral differences. These results are opposite to those reported for _Microtus_, a runway-dwelling group in which contacts probably do not increase with increasing population density (Pearson 1960; Carrol and Getz 1976). Levels of wounding in _Microtus_ appear to be related to whether a population is increasing or decreasing in density. High levels of wounding have been found in declining populations of _M_. _ochrogaster_ and _M_. _pennsylvanicus_, particularly late in the decline when densities are relatively low (Rose and Gaines 1976; Rose 1979). These results are nevertheless tentatively suspect, since both authors have failed to adjust their analyses for striking seasonal effects related to breeding intensity. Rose (1979) has also rather arbitrarily grouped what appears to be a series of annual cycles into phases of a superannual cycle, making his data particularly incomprehensible. These two studies have been quoted by Krebs (1978) as major evidence for Chitty's hypothesis, since they appear to reflect selection for aggressive (i.e. wounded) individuals as density declines from a peak. Interpretation of these two studies is nearly impossible without a more objective analysis of the data, and would certainly benefit from an understanding of how wounding is related to contact intensity and behavior.

Wounding in this study was not related to whether an individual won or lost in a behavioral trial. It is difficult to interpret this result, since the sources of wounding in the field are unknown. If fights in the field are as infrequent as they are in the neutral arena, wounding may be a poor measure of dominance in behavioral interactions. Threat and submissive behaviors are obviously important components of behavior in the neutral arena, and are presumably important in the field as well. Since they cannot be measured on dead animals, we have no way of knowing their importance in determining the fates of animals in the field. By using wounding as the only measure of behavioral interaction in field populations, we may be getting an extremely narrow and biased view of what is actually happening.

Electrophoresis

An essential ingredient of Chitty's hypothesis is the idea that qualitative changes in the population occur in association with variation in density. Electrophoretic work on the transferrin polymorphism of *C. gapperi* was specifically carried out to test the replicability of this phenomenon in *Clethrionomys*, since it has only been demonstrated in *Microtus* to date (Semeonoff and Robertson 1968; Tamarin and Krebs 1969; Gaines and Krebs 1971; Gaines *et al*. 1978; Kohn and Tamarin 1978). I also wished to test the repeatability of changes in gene frequency by comparing my results with an earlier study (Canham 1969), which implied cyclic changes similar to those occurring in

Microtus. Unfortunately, this comparison could not be made, as Canham (1969) made some errors in ageing voles, and also came to some incorrect conclusions about demography. When his data were regrouped into proper age-classes, sample sizes did not permit fitness calculations through successive generations. The changes in gene frequency he observed between years are significant, but it is impossible to determine where and when selection acted.

Striking changes in gene frequency did occur in *C. gapperi* in the course of this study. Similar fluctuations in gene frequency at the transferrin locus have occurred in four other studies, and are therefore probably indicative of a general phenomenon common to species that undergo superannual fluctuations in population density (Krebs and Myers 1974). These events are nevertheless only symptoms of the cycle, and do not necessarily cause demographic changes. This has been clearly demonstrated by Gaines *et al*. (1971) and LeDuc and Krebs (1975), who have manipulated gene frequencies in populations, and have been unable to alter the demography of their manipulated populations.

Previous studies of temporal variation in gene frequencies in microtines have been unable to determine the pattern of selection due to overlapping generations and relatively continuous breeding. Analyses of reproductive parameters (Kohn and Tamarin 1978) have also been unsuccessful in revealing universal differences in the reproductive value of different phenotypes. Birdsall (1974) and LeDuc and Krebs (1975) have concluded that much of the differential fitness of electrophoretic variants is due to differential survival from birth to trappable age, a parameter that can be inferred, but is impossible to monitor directly with current trapping techniques. My results partly agree with this conclusion, as major changes in gene frequency appeared to occur between generations, with frequencies remaining relatively stable within any particular generation in the trappable population. Selection nevertheless probably occurred between fall and spring in each year, either within generations or through differential survival of separate generations. Since I was unable to age animals in spring, I have no way of knowing which one of these alternatives is correct. Selection appeared to be acting on individual parameters that I could not measure, as phenotypes showed no striking differences in growth, reproduction, or behavior.

Selection at the transferrin locus involved two consistent factors that were independent of the population cycle; selection favoring the heterozygote in the early-summer mature "generation", and selection favoring the FF homozygote over winter. Seasonal selection on electrophoretic variants has also been observed in Mus (Berry et al. 1978), and in Apodemus (Leigh Brown 1977). Gill (1977) has observed both of these patterns in a very different polymorphic system, the buffy coat color system of M. californicus on Brooks Island. Heterozygous advantage may be a common feature of many populations (Smith _et al_. 1975, 1978). Seasonal selection may also be important, but has not been assessed in _Microtus_ due to the impossibility of ageing animals with continuous breeding.

The above trends appear to be independent of the population cycle itself, since they were repeated in nearly every year of observation (heterozygotes were not favored in 1977). A secondary trend associated with the cycle appears to involve selection for the Fast allele in increasing populations and selection for the Slow allele in decreasing populations. These trends are based on relatively few data points, but may reflect real processes considering the fact that data for these trends come from four separate sources (Canham 1969; McPhee 1977; Fuller 1969, 1977a, unpublished; this study). If correlations between gene frequency and density are in fact reliable, they provide one of the few tools available to biologists in the prediction of demographic change. Although processes responsible for gene frequency changes are still unknown, these results suggest at least three factors that are responsible for the changes seen:

(1) heterozygous advantage in reproductive cohorts,
(2) seasonal selection favoring one homozygote,
(3) balancing selection associated with population density.

Chitty's Hypothesis

Although Chitty's hypothesis was not explicitly tested in this study (Krebs 1978), I did examine a few of the essential components of the hypothesis. A brief summary of four critical points in the hypothesis follows:

1. Mutual interference increases with density.

This assumption seems reasonable for *C. gapperi*, given the increases in spatial overlap seen on the multiple capture grid, but may not apply to classically cyclic species of *Microtus* (Pearson 1960; Caroll and Getz 1976), and is therefore questionable.

2. Behavioral types exist.

Behavioral variability prevented an accurate assessment of this assumption. "Personality" differences were found in a few overwintered males, but it was not clear how these could be related to population regulation. Mature males occupied a low position within the population dominance hierarchy, and presumably were not critically involved in population regulation. Poor repeatability for behavioral scores also strongly argues against the existence of the behavioral type. Except for some differences in activity parameters in voles from cycling and noncycling populations (Rasmuson *et al*. 1977; Nygren 1978), there is no evidence to support the existence of behavioral types in microtines. Heritable behavioral differences in other rodents are nevertheless well established in the literature (Broadhurst *et al*. 1974; Guttman *et al*. 1975; Ebert and Hyde 1976;

Selmanoff *et al.* 1976; DeFries and Plomin 1978). Better methods of measuring individual behavior are sorely needed, as are breeding studies on the heritability of aggression.

3. *Quality varies with density.*

Changes in gene frequency at the transferrin locus of *C. gapperi* support this corollary of the hypothesis. Qualitative changes in the population appear to be a common feature of population cycles, but there are as yet no indications as to what these changes actually mean. Similarly, it is not known if these changes only occur in fluctuating populations (Smith *et al.* 1978).

4. *Behavior varies with density.*

This corollary of the hypothesis seems easy to test conceptually, but is very difficult to test in practice. Multivariate studies of behavior are rare (Krebs 1970; Svendsen and Armitage 1973; Turner and Iverson 1973; Conley 1976; Mihok 1976; Fairbairn 1978b), and have generally been difficult to interpret either because of weak methodology or insufficient sample sizes. Krebs (1970) has possibly found minor differences in male-male behavior associated with the population cycle in *Microtus*, whereas Turner and Iverson (1973) have found only seasonal trends. Conley (1976) has also found minor differences in behavior between high and low density years, but the matter is additionally complicated by significant behavioral changes associated with the density of a competing species. Behavioral profiles of red-backed voles in this study do not support the contention that behavior changes with density fluctuations. It can always be argued that I did not adequately test for behavioral differences, but I feel that this point is not justified. The years 1976 and 1977 provided an excellent contrast in population dynamics and yet did not contrast in behavior. In particular, high density in the fall of 1976, and the subsequent severe winter decline of 1976-77 should have revealed selection for aggressive animals in the overwintered generation of 1977. Contrary to this prediction, there were no differences in the behavior of overwintered males between years, and there were only minor differences in amicable behavior in overwintered females. This evidence strongly argues against behavioral differences between years, and is supported by general trends in spacing behavior and in levels of wounding. Individual parameters such as sex, age, and maturity were generally sufficient to account for much of the behavioral variability seen in this study.

Although Chitty's Hypothesis cannot be supported or rejected by the results of this study the weight of evidence against it is considerable. Behavioral changes associated with the population cycle may exist, but do not appear to be important in the relationships between animals in the "trappable" population. Behavior may still be important, but it obviously must act in ways that influence the recruitment of juveniles into the population, or influence the survival of animals through winter. Qualitative changes in the population appear to be more tenable as a hypothesis, but are poorly understood. Finally, the relationship between behavior and genetics appears to be particularly weak, although it may exist on the level of the genome as a whole (Smith *et al*. 1978). In order to understand the relationships between demography, behavior, and genetics, future studies will require a much more detailed understanding of the early life history of small rodents. Selection appears to be particularly intense before an animal is actually trapped by conventional methods, and it is therefore imperative that methods be changed to monitor this critical time in life. By only studying the trappable population, we may be missing the point entirely in our attempts to elucidate mechanisms of population regulation.

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Table 1. Trapping schedule for the multiple capture grid.

Rota	1976		1977	
1	May	9-13	May	8-12
2	May	23-27	May	22-26
3	June	6-10	June	5- 9
4	June	20-21†	June	19-23
5	July	4- 8	July	3- 7
6	July	18-22	July	17-21
7	August	1- 5	July 31-August 2†	
8	August	15-19	August	14-18
9	August	29-31†	September	4- 8
10	September	22-27††	September	18-22

† Shortened rotas (normal period is five days).

†† Each half of the grid was trapped for three days.

Table 2. Categories used in habitat surveys.

Trees

Larix laricina
Picea glauca
Picea mariana
Pinus banksiana
Populus tremuloides

Shrubs

Alnus crispa
Betula glandulosa
Juniperus communis
Potentilla fruticosa
Rosa spp.
Salix spp.
Shepherdia canadensis
Viburnum edule

Ground Cover

Graminoids and sedges
Mosses
Lichens (mostly *Cladonia*)

Miscellaneous

Arctostaphylos rubra
Arctostaphylos uva-ursi
Cornus canadensis
Empetrum nigrum
Epilobium angustifolium
Equisetum spp.
Geocaulon lividum
Hedysarum alpinum
Ledum groenlandicum
Linnaea borealis
Mitella nuda
Pyrola spp.
Vaccinium vitis-idaea

Ground Moisture
Microrelief

Table 3. Minimum 14-day survival rates between successive rotas on the multiple capture grid.

		Rota								
Age	Year	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10
OW†	1976	0.56	0.91	0.89	0.61	0.64	0.89	0.63	0.58	1.00
		(18)	(21)	(21)	(19)	(14)	(9)	(8)	(5)	(3)
	1977	0.82	0.85	0.80	0.77	0.80	1.00	1.00	0.71	1.00
		(11)	(13)	(15)	(13)	(10)	(6)	(6)	(5)	(3)
Young	1976					0.57	0.77	0.86	0.79	0.85
						(14)	(22)	(29)	(41)	(64)
	1977					0.00	0.62	1.00	0.73	0.80
						(3)	(11)	(13)	(16)	(25)

Note: Sample sizes are given in parentheses, and refer to the number of animals known alive at the start of each period.

† OW = Overwintered

Table 4. Lumped 14-day minimum survival rates for the multiple capture grid for animals in the "trappable" population.

Age	Breeding Status	Sex	Year	N(t)	N(t+14)	% Survival	X^2†
OW	Mature	M	1976	75	58	77	0.0
			1977	39	30	77	
		F	1976	43	27	63	6.7*
			1977	45	39	87	
YG	Mature	M	1976	23	19	83	0.1
			1977	25	20	80	
		F	1976	33	23	70	0.0
			1977	19	13	68	
YG	Immature	M	1976	74	58	78	0.7
			1977	16	11	69	
		F	1976	41	37	90	
			1977	8	6	75	

† This X^2 test must be interpreted with caution since an animal can be tabulated more than once in each category.

* $P < 0.01$

Table 5. Timing of litters estimated from actual births in captivity to live-trapped females, and extrapolated dates of birth from visibly pregnant snap-trapped females.

Category		Day of Year	N	SD	Min	Max
Overwintered						
First	1976	164	19	16.58	143	198
	1977	154	19	11.36	139	179
Second	1976	201	42	18.92	172	241
	1977	191	26	16.14	166	232
Third	1976	210	4	11.28	199	224
	1977	219	3	16.00	203	235
Young						
First	1976	211	17	10.57	196	232
	1977	219	13	9.20	211	225
Second	1976	225	11	6.25	211	240
	1977	223	6	10.50	211	237

Note: Second litter category probably includes roughly 10-20% third litters due to disappearance of placental scars.

Table 6. Analysis of Variance of the effects of year, parity, and age on litter size at birth.

Source of Variation	Sum of Squares	DF	Mean Square	F	P
Year	4.12	1	4.12	3.59	0.062
Parity	2.07	1	2.07	1.80	0.183
Age	6.19	1	6.19	5.39	0.023
Year X Parity	1.53	1	1.53	1.33	0.251
Year X Age	0.29	1	0.29	0.25	0.617
Parity X Age	4.48	1	4.48	3.90	0.051
Year X Parity X Age	1.84	1	1.84	1.60	0.209
Explained	27.17	7	3.88	3.38	0.003
Residual	98.76	86	1.15		
Total	125.93	93	1.35		

Age	No. of Litter	Mean	SD	N
Overwintered	First	5.53	1.31	19
	Second	6.19	0.93	52
Young	First	5.42	1.06	23
	Second	4.67	1.63	6

Note: Third litters were excluded due to small sample sizes.

Table 7. Dates for the division of the year into six time periods based on female reproduction.

Period	Description	Criteria	1976	1977
1	Pre-mating	22+ days prior to median date of first OW litter	<139	<138
2	OW females pregnant	From 1 to median date of first OW litter	139-161	138-160
3	OW females wean first litters	From 2 to 18 days later	162-179	161-178
4	YG maturing and YG females pregnant	From 3 to median date of first YG litter	180-214	179-219
5	YG females wean first litters	From 4 to last birth recorded overall	215-241	220-240
6	Post breeding late litters being weaned	From 5 on	>241	>240

Table 8. Comparison of age structure between years in voles captured on Sherman traplines.

	Period 4		Period 5		Period 6	
M^2 Age class	1976	1977	1976	1977	1976	1977
% Open groove	22.4	9.4	16.7	10.3	8.6	1.0
% Closed	31.0	26.4	41.0	53.4	77.6	71.4
% Roots formed	10.3	11.3	17.9	29.3	10.3	18.1
% Overwintered	36.2	52.8	24.4	6.9	3.4	9.5
Sample Size	58	53	78	58	58	105
Effort†	22.4	24.6	11.2	15.7	6.7	16.7
Chi-square	4.84		9.94		9.50	
Probability	0.18		0.02		0.02	

Note: Absolute ages are roughly < 1 month (open grooves), 1-2 months (closed grooves), 2-4 months (roots formed).

† Units are 100 trap nights.

Table 9. Recruitment, age structure in the fall, and probability of surviving to the fall for young caught on the multiple capture grid.

Rota of first capture	No. first captures†		No. surviving to rota 10		Probability of surviving	
	1976	1977	1976	1977	1976	1977
5	13	3	3	0	0.23	0.00
6	14	9	7	1	0.50	0.11
7	13	6	5	3	0.38	0.50
8	16	6	11	5	0.69	0.83
9	31	15	21	12	0.68	0.80
10	71	7	71	7		

† Trap deaths excluded.

Table 10. Analysis of Covariance of the regression between M^2 root length in overwintered voles and day of the year at autopsy.

Year	Intercept	Slope	r^2	F	DF1	DF2	P
1976	0.604	0.00472	0.312	39.88	1	88	0.000
1977	0.533	0.00456	0.494	91.83	1	94	0.000

Null Hypothesis	F	DF1	DF2	P
Equal Variance	1.39	88	94	0.114
Equal Slope	0.03	1	182	0.849
Equal Intercept	11.12	1	183	0.001

Table 11. Sex distribution by time periods for animals caught on the multiple capture grid and on Sherman traplines.

			Young of the year			
Time	Overwintered		Mature		Immature	
Period	Female	Male	Female	Male	Female	Male
1976						
1	12	19	-	-	-	-
2	21	22	-	-	-	-
3	16	20	-	-	0	2
4	16	15	21	22	7	13
5	13	10	21	13	28	50*
6	2	2	8	6	56	104*
1977						
1	17	24	-	-	-	-
2	20	23	-	-	-	-
3	23	17	1	1	-	-
4	19	18	9	7	3	7
5	6	4	19	13	10	12
6†	3	10	9	11	29	64*

* Deviates significantly at the 5% level from 1:1 sex ratio (Chi-square test).

† About 1/3 of these animals were caught in Longworth traps.

Table 12. Sex distribution at first capture in young caught on the multiple capture grid, and distribution by M^2 age-classes in young caught on Sherman traplines.

	Immature			Mature		
	Female	Male	Chi-square	Female	Male	Chi-square
At first capture						
1976	57	85	5.13*	9	9	-
1977	9	20	3.45	9	11	0.05
By age-classes						
Open grooves	17	16	0.00	4	8	0.75
Closed grooves	50	126	31.96**	19	21	0.03
Roots formed	4	8	0.75	41	15	11.16**
Total	71	150	27.53**	64	44	3.34

* $P < 0.025$ (Yates correction applied).

** $P < 0.001$

Table 13. Regression analyses of age with M^2 tooth measurements in voles of known age raised in outdoor pens.

Variable	Constant	Slope	SE	F	N
1. Open groove					
Tooth length	-27.6	17.3	1.94	79.16	34
2. Closed groove (Immature)					
Tooth length	127.0	-17.9	3.44	26.94	100
log Groove closure		24.8	2.81	78.30	
3. Closed groove (Mature)					
Tooth length	93.9	-10.5	6.10	2.99	44
log Groove closure		8.6	5.34	2.60	

Category	r^2	Error in days Mean	Error in days Max	P†
Open groove	0.71	2.6	8.3	0.000
Closed groove				
Immature	0.56	3.7	11.5	0.000
Mature	0.14	3.5	15.6	0.043

Note: Age (days), other measurements (mm).

† Significance level of (multiple) regression (F test).

Table 14. Multiple regression analyses of growth in voles raised in outdoor pens in 1977.

Variable	Constant	Slope	SE	F	r^2	N
1. Weight at weaning (g)						
	6.372					
Litter size		-1.084	0.120	82.22	0.39	179
Condition mother		8.531	1.387	37.84		
Day of year at birth		0.023	0.005	21.21		
2. Weight gained after weaning (g)						
	8.677					
Days in pen		0.140	0.023	37.13	0.31	132
Sex†		-1.567	0.461	11.56		
Weight weaning		-0.236	0.117	4.07		
3. Body length (mm)						
	82.142					
Age in days		0.329	0.039	69.68	0.37	124
Slow Tf††		-2.255	0.845	7.12		
4. Condition†††						
	0.155					
Age in days		0.009	0.001	44.38	0.45	118
Weight weaning		0.034	0.006	35.70		
Sex		-0.053	0.019	7.67		
Slow Tf		0.073	0.028	6.89		

Note: F statistic refers to partial F test (all values with $P < 0.05$), r^2 is multiple r^2 of entire regression.

† Male=1, Female=0

†† Homozygote Slow-Slow transferrin genotype (dummy variable relative to heterozygote)

†††

$$\text{Condition} = \frac{\text{Weight}}{\text{Body Length}^{0.67}}$$

Table 15. Distribution of pairs in multiple captures.

Year	M-M	M-F	F-F	Probability Male	X^2
Mature with Mature					
1976	9 (13.9)	30 (20.1)	2 (6.9)	0.59	10.1*
1977	13 (14.6)	20 (16.8)	3 (4.6)	0.64	1.3
1978	0 (2.7)	12 (6.5)	0 (2.7)	0.50	-
Total	22 (31.4)	62 (43.1)	5 (14.4)	0.60	17.3*
Immature with Immature					
1976	36 (35.7)	35 (35.7)	9 (8.7)	0.67	0.0
1977	3 (4.8)	10 (6.4)	0 (1.8)	0.62	-
Total	39 (40.6)	45 (41.9)	9 (10.6)	0.66	0.5

Note: Expected values are in parentheses and are calculated from the hypergeometric distribution [e.g. expected mature male with mature male total is (106•105/178•177)•89].

* $P < 0.005$

Table 16. Distribution of pairs in multiple captures of mature voles with immatures.

	Mature Male with		Mature Female with		
	Immature M	Immature F	Immature M	Immature F	X^2
1976	12 (15.5)	12 (8.5)	17 (13.5)	4 (7.5)	4.7*
1977	10 (10.5)	7 (6.5)	6 (5.5)	3 (3.5)	-
Total	22 (26.0)	19 (15.0)	23 (19.0)	7 (11.0)	4.0*

Note: Expected values are in parentheses and are calculated from the binomial distribution.

* $P < 0.05$

Table 17. Indices of dispersion (Observed nearest neighbor distance/ Expected nearest neighbor distance) calculated from centers of activity of animals caught on the multiple capture grid.

		Rota									
	Year	1	2	3	4	5	6	7	8	9	10
Total	1976	0.9	0.9	0.9	1.3	0.8	1.0	0.9	1.1	0.9	0.9*
	1977	0.6*	0.8	1.0	1.0	1.0	1.0	1.3*	1.3*	1.1	1.0
	1978	0.7*									
Reproductive†											
M	1976	0.9	1.1	1.1	1.4	1.1	1.4	1.2	1.1	-	-
	1977	-	1.0	1.0	-	1.3	1.2	1.0	1.0	-	-
	1978	1.6*									
F	1976	0.8	1.6*	1.7*	1.7*	1.3	0.9	1.5*	1.5*	1.7*	-
	1977	-	1.5*	1.3	1.2	0.8	1.2	1.6*	1.6*	-	-
	1978	1.6*									
Immature											
M	1976					2.0*	0.7	1.2	1.1	1.0	1.0
	1977							-	-	1.0	1.2
F	1976					-	-	-	1.4	1.0	1.0
	1977								-	1.2	1.1

Note: Values > 1 indicate that centers of activity are uniformly spaced whereas values < 1 indicate that they are clumped.

Indices are based on a minimum of six animals, dashes represent insufficient sample sizes.

* P < 0.05

† Mature animals excluding quiescents.

Table 18. Transferrin phenotypes from various studies at Heart Lake, N.W.T. (1966-1968: reclassified data of Canham (1969); 1974: McPhee (1977); 1975: this study and McPhee (1977); 1976-1978: this study).

	Density			Transferrin†				
Year	May	August	Age Class	Freq F	SS	SF	FF	N
1966	L	M	OW	0.65	0.100	0.500	0.400	10
			Young	0.61	0.189	0.405	0.405	37
1967	M	L	OW	0.58	0.157	0.529	0.314	51
			Young	----	0.333	0.556	0.111	9
			Unknown	----	0.000	0.500	0.500	2
1968	L	L	OW	----	0.200	0.400	0.400	5
			Young	0.51	0.200	0.571	0.229	35
			Unknown††	0.44	0.170	0.532	0.298	47
1974	H	H	OW	0.29	0.500	0.429	0.071	14
			Young	----	0.000	0.667	0.333	3
1975	L	M	OW	0.49	0.275	0.471	0.255	51
			Young	0.41	0.279	0.623	0.098	61
1976	M	H	OW	0.50	0.156	0.688	0.156	77
			Young	0.54	0.180	0.556	0.263	133
1977	L	M	OW	0.62	0.158	0.453	0.389	95
			Young	0.51	0.264	0.451	0.285	144
1978	L	M	OW	0.52	0.286	0.476	0.238	21
			Young	0.54	0.077	0.920	0.000	13

Note: L density (< 2.0 per 100 Trap Nights), M (2.0 to 4.0), H (> 4.0) from Figure 16.

† S=Slow, F=Fast

†† Animals caught in August, mostly young of the year

Table 19. Transferrin phenotypes of litters born in captivity to wild-caught females in 1976 and 1977, and tests of Incomplete Family Data after Cooper (1968).

Number of litters	Mother's phenotype	Offspring FF	Offspring SF	Offspring SS
11	FF	26	17	
15	SF	21	33	7
7	SS		20	12

Statistical Test	X^2	Significance
(a) Expected 1:1 ratio of homozygotes to heterozygotes in heterozygous litters	0.26	$0.90 > P > 0.75$
(b) Heterogeneity of individual gametic ratios (2 DF)	4.93	$0.10 > P > 0.05$
(c) Agreement with Hardy-Weinberg expectation	1.02	$0.50 > P > 0.25$

Table 20. Behaviors recorded in the neutral arena tests.

Behavior	Freq†	Brief Description
		Approach Components
Nn	1.85	Nasonasal: investigation and (or) sniffing of nasal region of other vole, includes the category Neu, which always precedes it
Neu	1.65	Neutral: casual approach indistinguishable from normal exploratory behavior, not followed by Nn or Na
Str	0.98	Stretch: specific postural approach, body and head form a line, front slightly elevated, ears directed forward, hair on back often erect (Johst 1967)
Na	0.59	Nasoanal: investigation and (or) sniffing of anal or genital region of other vole, includes the category Neu, which always precedes it
Hes	0.19	Hesitant: approach is characterized by discontinuity, animal stops, slows down, or changes direction
		Termination Components
Wit	2.07	Withdrawal: vole walks away from encounter
Ret	1.81	Retreat: vole runs quickly away
Avo	0.05	Avoid: vole changes direction on approach to avoid other vole
		Encounter Components
Voc††	3.75	Vocalization: squeak or squeal type
Rap	1.70	Raise partially: paw lifts into a crouching posture (Johst 1967)
Paw	1.50	Pawbeat: beat opponent with both paws
Sub	1.25	Submissive: specific posture with head and ears down, eyes often closed, occasionally used on approach
Tur††	0.94	Turn away: vole turns head and then body away from opponent, head usually oriented downwards
Pw1	0.91	Pawbeat 1: beats opponent with one paw, sometimes ending with paw resting on opponent's head

Table 20. (continued)

Rai	0.58	Raise: frontal rears into full upright posture (Johst 1967)
Hud	0.57	Huddle: Huddles with other vole
Fol	0.50	Follow: walks after withdrawing vole
Cha	0.47	Chase: runs after retreating vole
Got	0.45	Groom other: grooms opponent
Grm	0.37	Groom: grooms self
Att	0.27	Attack: leaps at other vole, scored whether successful in making contact or not
Fgt††	0.11	Fight: fights in a tumbling ball with other vole

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† Frequency of behavior per trial per animal (divide by six to get frequency per encounter).

†† Behaviors different from those scored in 1975 (Mihok 1976, Table 3).

Table 21. Correlation coefficients between the behavioral variables over 1628 OTUs (decimals omitted).

Variable	Nn	Neu	Str	Na	Hes	Wit	Ret	Avo	Voc	Rap	Paw	Sub	Tur
Nn	...												
Neu	-23	...											
Str	-24	-08	...										
Na	74	-17	-16	...									
Hes	-11	-02	00	-08	...								
Wit	45	08	-17	36	01	...							
Ret	-23	10	14	-17	09	-28	...						
Avo	-07	04	-05	-06	33	-07	03	...					
Voc	-07	-06	03	-06	-05	-03	02	-03	...				
Rap	-05	-11	12	-04	-06	00	-08	-06	64	...			
Paw	-10	-05	05	-07	-04	-05	03	-02	69	56	...		
Sub	25	-06	-11	23	-04	21	-15	-04	-01	-03	-05	...	
Tur	-01	08	00	02	00	07	-09	-03	-03	12	10	42	...
Pw1	01	-04	01	01	-05	09	-07	-03	56	54	24	-03	-03
Rai	-13	01	15	-10	-01	-09	14	01	26	18	46	-04	13
Hud	70	-18	-19	60	-08	30	-21	-06	-01	00	-07	28	00
Fol	48	-13	-12	55	-07	35	-12	-05	-03	-03	-05	39	04
Cha	-07	-09	08	-05	-04	-09	07	-01	00	-07	04	-03	01
Got	61	-11	-16	54	-08	33	-16	-05	-04	-01	-07	26	01
Grm	42	-07	-07	35	-05	23	-15	-05	15	26	13	24	24
Att	-11	05	20	-08	-05	-20	10	-01	03	-06	06	-07	-02
Fgt	-08	00	08	-06	-03	-09	40	03	11	-04	13	-02	02

	Pw1	Rai	Hud	Fol	Cha	Got	Grm	Att	Fgt
Pw1	...								
Rai	04	...							
Hud	03	-09	...						
Fol	00	-07	39	...					
Cha	-03	22	-07	-04	...				
Got	05	-07	51	35	-05	...			
Grm	16	05	43	22	-03	34	...		
Att	-03	25	-10	-06	74	-07	-06	...	
Fgt	00	33	-07	-04	57	-06	-03	61	...

Table 22. Quartimax rotated solution from the Alpha Factor Analysis of the 22 square root transformed variables in Table 20 (N=1628).

Variable	Factor							
	AMI	THR	AGG	SBT	AVD	BOX	APV	h²
Nn	.91	-.05	-.03	-.12	-.05	-.02	-.08	.85
Neu	-.17	-.06	.04	.05	-.01	.02	.55	.34
Str	-.25	.06	.12	.03	-.06	.08	-.23	.15
Na	.81	-.05	-.01	-.06	-.03	.05	-.11	.67
Hes	-.08	-.04	-.04	.02	.58	.02	-.03	.35
Wit	.49	.03	-.04	.06	.00	-.18	.25	.34
Ret	-.26	-.05	.11	-.09	.05	.50	-.01	.34
Avo	-.06	-.03	.01	-.03	.57	.01	.04	.33
Voc	-.01	.88	.01	-.07	-.01	.08	.03	.80
Rap	-.02	.84	-.06	.07	-.05	-.13	-.16	.76
Paw	-.06	.70	.06	.12	-.01	.25	-.01	.57
Sub	.40	-.05	-.02	.46	-.02	-.04	.01	.38
Tur	.05	.06	.01	.83	-.01	-.02	.05	.70
Pw1	.06	.56	-.02	-.10	-.03	-.16	.02	.35
Rai	-.11	.31	.27	.16	.00	.32	-.05	.31
Hud	.75	.00	-.03	-.02	-.03	-.02	-.09	.57
Pol	.59	-.05	-.01	.10	-.03	.01	-.04	.36
Cha	-.05	-.02	.80	.00	-.03	.01	.06	.65
Got	.66	.00	-.01	-.01	-.03	-.01	-.01	.44
Grm	.46	.24	.00	.20	-.02	-.03	-.04	.31
Att	-.12	-.01	.94	-.02	-.04	-.02	-.09	.91
Pgt	-.04	.06	.66	-.01	.02	.47	.05	.66
Eigenvalue	8.00	4.53	3.14	1.98	1.81	1.49	1.06	
% Variance	36.3	20.6	14.3	9.0	8.2	6.8	4.8	
r²†	.93	.93	.94	.77	.52	.62	.47	

Note: Variables are in the same order and groupings as in Table 20.

† Coefficient of determination for the relationship between factor score estimate and hypothetical factor.

Table 23. Mean factor scores of the four standard voles of each sex against all opponents.

Factor	Mean	SE	Min	Max	F	P
Standard Males (N=91)						
AMI	-0.35	0.040	-0.82	2.47	3.70	0.015
THR	-0.11	0.069	-0.75	3.49	2.32	0.081
AGG	0.18	0.100	-0.41	4.05	6.56	0.001
SBT	0.38	0.127	-0.69	6.22	3.50	0.019
AVD	-0.01	0.057	-0.36	2.94	0.02	0.997
BOX	0.20	0.097	-1.94	4.03	0.88	0.454
APV	0.22	0.084	-2.67	2.33	2.71	0.050
Standard Females (N=54)						
AMI	0.22	0.124	-0.64	3.07	2.51	0.069
THR	-0.32	0.048	-0.69	1.08	2.76	0.052
AGG	-0.22	0.011	-0.37	0.04	1.26	0.298
SBT	-0.16	0.061	-0.90	1.42	0.70	0.555
AVD	-0.06	0.074	-0.29	2.99	1.19	0.322
BOX	-0.05	0.042	-0.66	0.61	1.21	0.317
APV	-0.04	0.095	-1.48	1.52	1.40	0.253

Note: F test is for the null hypothesis that the mean factor scores of each standard vole are equal.

Table 24. Reliability of behavioral measures in terms of the factor scores for animals completing three trials against opponents of the same sex, age and reproductive condition (N=149).

	Correlation Coefficients			Cronbach's
Factor	Trial 1&2	Trial 1&3	Trial 2&3	Alpha
AMI	0.538*	0.367*	0.455*	0.690
THR	0.216*	0.094	0.178*	0.360
AGG	0.124	0.130	0.407*	0.407
SBT	0.238*	0.428*	0.256*	0.549
AVD	0.061	-0.050	-0.041	-0.038
BOX	0.153*	-0.003	0.238*	0.251
APV	0.015	0.039	0.214*	0.242

* r > 0 at 5% level of significance.

Table 25. Behavioral profiles of clusters derived from UPGMA analysis of behavior in categories of the OTUs relating to sex, age, and sexual maturity (see Fig. 24).

Cluster		Factor						
Code	Key†	AMI	THR	AGG	SBT	AVD	BOX	APV
A	VAR	-0.20	-0.01	-0.11	-0.08	-0.01	0.04	-0.06
B	VAR	0.07	-0.25	-0.08	-0.14	-0.10	0.01	0.12
C	agg	-0.30	0.05	0.31	-0.09	0.02	-0.16	-0.14
D	sbt	-0.22	-0.16	-0.03	0.33	0.05	0.03	0.14
E	AMI	0.46	-0.19	-0.17	-0.09	-0.07	-0.14	0.00
F	AGG	-0.22	0.05	0.89	0.42	-0.22	-0.66	-0.23
G	ami	0.93	0.63	-0.18	-0.50	-0.16	0.39	0.48
H	THR	-0.26	1.19	0.14	-0.28	-0.07	0.07	-0.14
I	SBT	0.03	-0.32	-0.04	1.50	0.26	0.25	0.44

† Keyword symbolic of the emphasis of behavior in each cluster, VAR=Variable (none emphasized), lower case used when factor is weakly emphasized.

Table 26. Type of behavior shown in combinations relating to sex, age and sexual maturity (see Table 25 for explanation of keywords).

		Male					Female		
		OW	Y+	Y-			OW	Y+	Y-
Male	OW	agg	agg	sbt	Male	OW	SBT	SBT	VAR
	Y+	VAR	VAR	VAR		Y+	sbt	sbt	AMI
	Y-	THR	VAR	AMI		Y-	VAR	AMI	AMI
		Female					Male		
		OW	Y+	Y-			OW	Y+	Y-
Female	OW	VAR	agg	AGG	Female	OW	THR	AGG	sbt
	Y+	VAR	VAR	VAR		Y+	THR	agg	AMI
	Y-	ami	VAR	AMI		Y-	VAR	AMI	AMI

Note: Keyword refers to behavior of row vs column.

Table 27. Dominance hierarchy within the population as determined by wins and losses based on the Dominance variable.

Sex	Age	Breeding Status	F OW +	F Y +	M Y −	F Y −	M OW +
F	Y	Mature	30:10*				
M	Y	Immature	2:2	11:10			
F	Y	Immature	4:3	20:15	21:13		
M	OW	Mature	38:5*	5:2	25:9*	5:4	
M	Y	Mature	8:2	9:5	23:17	3:1	13:11

* Significantly different from 1:1 ratio (Chi-square test).

Note: Values given are wins: losses to column.

Table 28. Significance of behavioral differences between years in terms of Hotellings T^2 test on the seven factor scores.

Sex Type	Age and Breeding Category	T^2	DF1	DF2	F	P
F vs F	OW vs OW	24.33	7	168	3.356	0.002
	Y+	12.87	7	32	1.548	0.187
	Y+ vs OW	19.16	7	32	2.305	0.051
	Y+	15.52	7	58	2.009	0.069
	Y-	18.75	7	27	2.191	0.067
	Y- vs Y+	11.56	7	27	1.352	0.265
	Y-	21.01	7	60	2.729	0.016
M vs M	OW vs OW	7.61	7	166	1.049	0.399
	Y+	11.43	7	16	1.187	0.364
	Y-	13.45	7	26	1.561	0.191
	Y+ vs OW	17.66	7	16	1.835	0.149
	Y-	6.41	7	32	0.771	0.616
	Y- vs OW	31.46	7	26	3.652	0.007
	Y+	22.31	7	32	2.684	0.026
	Y-	25.68	7	216	3.570	0.001
F vs M		10.78	7	138	1.476	0.181
M vs F		10.91	7	138	1.494	0.174

Table 29. Behavioral profiles between years for categories with large sample sizes showing significant variation between 1976 and 1977.

		Factor						
Year		AMI	THR	AGG	SBT	AVD	BOX	APV
OW F vs OW F (N=94,82)								
1976	Mean	-0.362	-0.023	0.080	0.003	0.023	0.088	-0.086
	SD	0.315	0.581	-0.923	0.464	0.716	0.967	0.766
1977	Mean	-0.140	-0.021	-0.141	-0.016	-0.077	-0.129	-0.051
	SD	0.581	0.761	0.455	0.688	0.458	0.496	0.643
	P*	0.002	0.984	0.050	0.832	0.281	0.069	0.207
Y- F vs Y- F (N=34,34)								
1976	Mean	0.499	-0.304	-0.177	-0.022	0.178	-0.096	0.107
	SD	0.901	0.422	0.096	0.459	0.996	0.273	0.581
1977	Mean	0.414	-0.248	-0.232	-0.267	-0.146	0.024	-0.173
	SD	1.765	0.495	0.127	0.590	0.191	0.411	0.722
	P*	0.804	0.618	0.047	0.060	0.067	0.162	0.083
Y- M vs Y- M (N=126,98)								
1976	Mean	0.716	-0.086	-0.135	0.024	-0.260	-0.178	0.051
	SD	1.463	0.673	0.196	0.665	0.425	0.399	0.560
1977	Mean	0.506	-0.093	-0.193	-0.234	-0.129	-0.077	-0.025
	SD	1.586	0.642	0.146	0.548	0.189	0.358	0.679
	P*	0.305	0.938	0.015	0.002	0.026	0.051	0.357

* Probability that the means are equal on a two-tailed t-test.

Table 30. Discriminant Functions Analysis of the habitat in which an animal was caught, based on groups consisting of winners (won 2 or 3 trials) and losers (won 0 or 1 trial against opponents of the same sex, age-class and sexual maturity).

Function	Eigenvalue	% Variance	Canonical Correlation	Significance
1	0.203	100	0.410	0.047

Habitat Variable	Standardized Coefficient
Graminoids and Sedges	-0.587
Picea glauca	-0.434
Microrelief	-0.364
Alnus crispa	-0.296
Mosses	-0.243
Vaccinium vitis idaea	-0.149
Juniperus communis	-0.120
Pinus banksiana	-0.076
Ledum groenlandicum	0.184
Lichens	0.251
Ground moisture	0.345
Shepherdia canadensis	0.486
Rosa spp.	0.637

Group centroids Winners: -0.425 Losers: 0.394

Note: Many of the variables in Table 2 were eliminated due to lack of variation across groups.

67% of the animals are correctly classified by the discriminant function.

Table 31. Multiple regression analysis of the number of captures at the trap stations on the multiple capture grid in 1977 with habitat variables.

Variable	Constant	Slope	SE	F	r^2
	7.569				0.33
Alnus crispa		1.799	0.340	28.00	
Graminoids & sedges		2.376	0.824	8.31	
Picea glauca		-3.535	1.262	7.85	
Lichens		-1.929	0.794	5.90	

Note: Number of captures of *Peromyscus maniculatus* was also included as an independent variable in the original stepwise analysis.

Table 32. Distribution of captures on the multiple capture grid among habitat types.

		% Captures in Habitat Type†					
Year	Rotas	A	B	C	D	N	X^2
Random Expectation		31.4	47.1	16.5	5.0		
1976	1- 4	19.8	63.8	14.3	2.1	293	35.8
	5- 9	28.6	59.6	7.9	3.9	718	59.4
	10	24.0	57.0	13.6	5.4	317	14.1
1977	1- 4	36.3	53.4	9.3	1.0	292	23.2
	5- 9	22.9	63.9	8.6	4.6	524	63.7
	10	14.8	73.8	9.0	2.4	210	60.2
1978	1	25.8	70.8	3.4	0.0	89	25.2

Note: All X^2 values with $P < 0.025$.

† A: *Pinus banksiana* woodland
B: *Picea glauca* - *Pinus banksiana* forest
C: Dense *Picea glauca* forest
D: Miscellaneous

Classification after Wells (1976).

Table 33. Behavicral changes in females associated with pregnancy.

		Factor						
Category		AMI	THR	AGG	SBT	AVD	BOX	APV
Analysis of Variance								
F vs F	F	2.405	1.003	3.030	3.785	0.376	1.821	5.742
(N=318)	P	0.092	0.368	0.049	0.024	0.687	0.164	0.004
F vs M	F	0.600	0.443	4.326	0.690	0.369	3.825	0.092
(N=70)	P	0.552	0.644	0.017	0.505	0.693	0.027	0.912

Duncan's Multiple Ranges

	F vs F			F vs M	
	AGG	SBT	APV	AGG	BOX
Quiescent	-0.093	-0.187	-0.032	-0.269	0.460
Pregnant	-0.003	-0.040	-0.090	0.174	-0.164
Lactating	0.204	0.082	0.227	0.908	-0.685

Table 34. Comparison of behavioral scores relative to survival to the next rota and home range size for animals removed from the behavioral grid and paired with four standard opponents.

	Survive (16)		Do not Survive (6)		
Factor	Mean	s^2	Mean	s^2	t
AMI	-0.28	0.102	0.10	0.659	0.80
THR	0.46	0.662	-0.37	0.107	2.40*
AGG	0.02	0.273	1.05	3.881	1.99
SBT	-0.12	0.061	-0.27	0.023	1.43
AVD	-0.08	0.057	-0.11	0.037	0.28
BOX	0.14	0.361	-0.43	0.902	1.70
APV	0.10	0.301	0.17	0.310	0.25

	Large range (8)†		Small range (11)		
Factor	Mean	s^2	Mean	s^2	t
AMI	-0.37	0.053	-0.14	0.142	1.51
THR	0.45	0.861	0.30	0.526	0.40
AGG	-0.02	0.244	0.68	2.432	1.22
SBT	-0.04	0.097	-0.23	0.028	1.76
AVD	-0.08	0.039	-0.12	0.071	0.38
BOX	-0.01	0.238	-0.17	0.982	0.43
APV	-0.02	0.155	0.34	0.370	1.46

† Large range represents animals with Adjusted Range Lengths greater than the population mean, and small range represents animals with ARLs smaller than the population mean (only animals with more than one capture are included in the analysis).

* $P < 0.05$

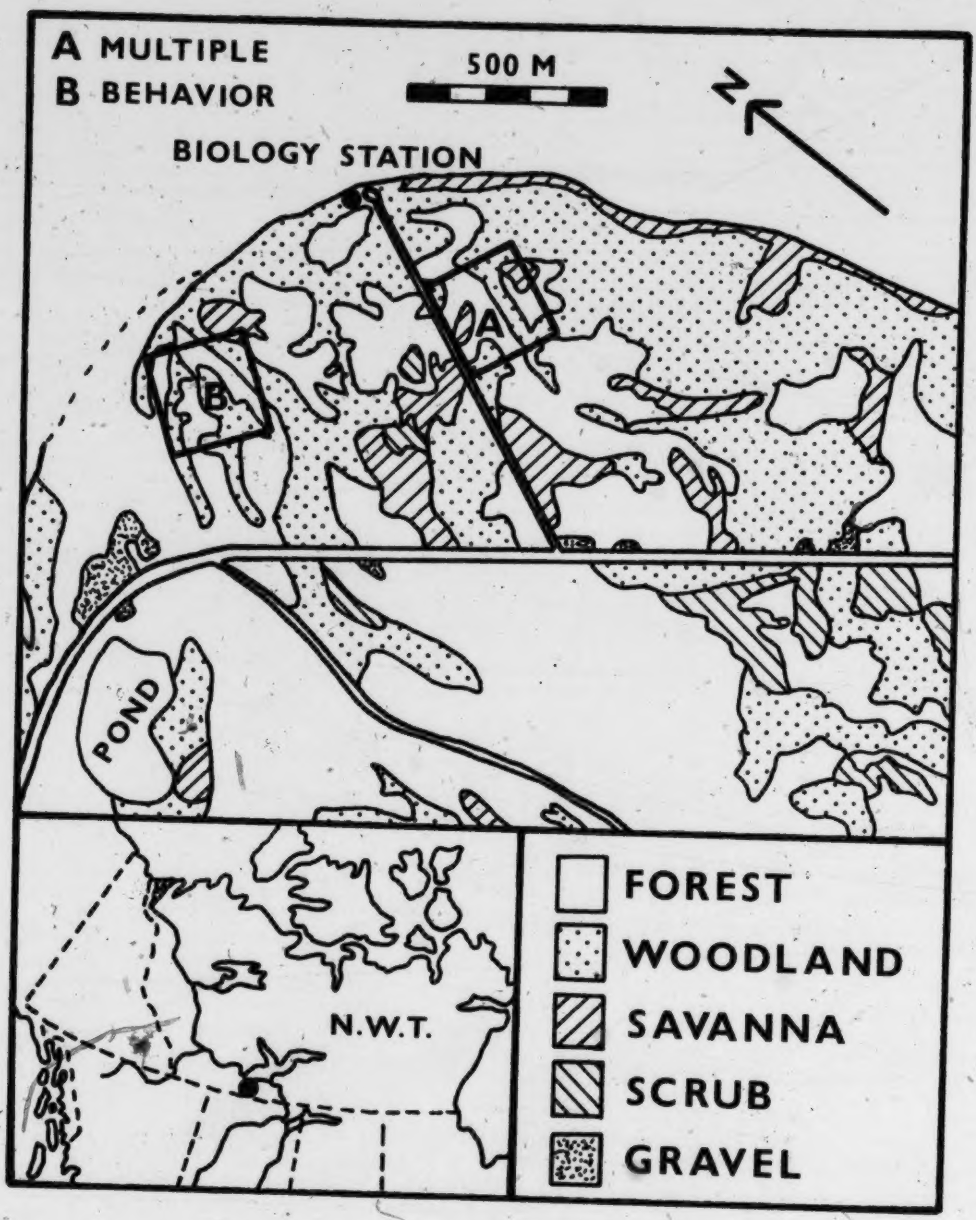
A MULTIPLE
B BEHAVIOR
500 M
N
BIOLOGY STATION
A
B
POND
N.W.T.
FOREST
WOODLAND
SAVANNA
SCRUB
GRAVEL

Figure 1. Map of the area around the Heart Lake Biological Station at km 130 on the Mackenzie Highway, showing the locations of the live-trapping grids (vegetation after Talbot 1978).

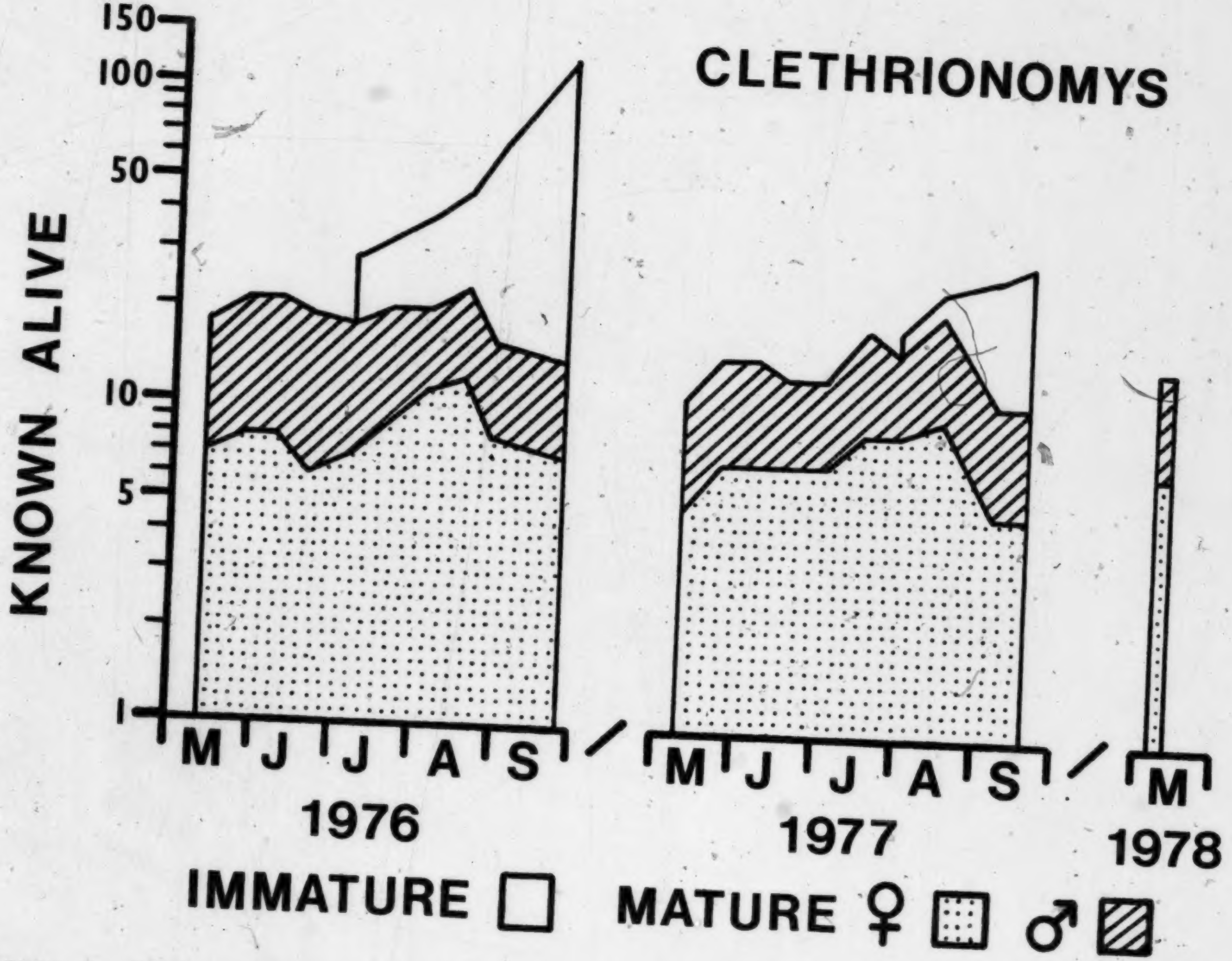

Figure 2. Minimum number of Clethrionomys gapperi known to be alive on the multiple capture grid.

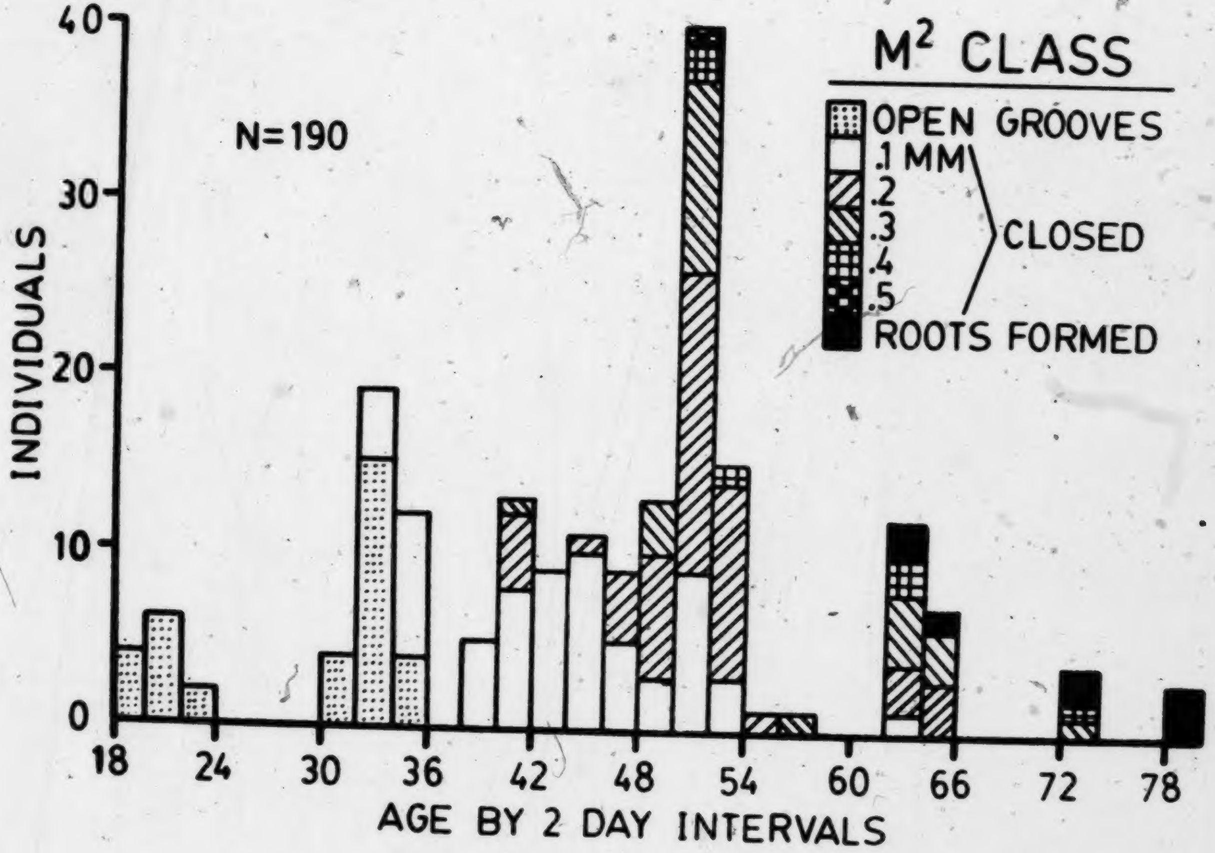

Figure 3. Root development in the second upper molar (M^2) in animals of known age raised in outdoor pens.

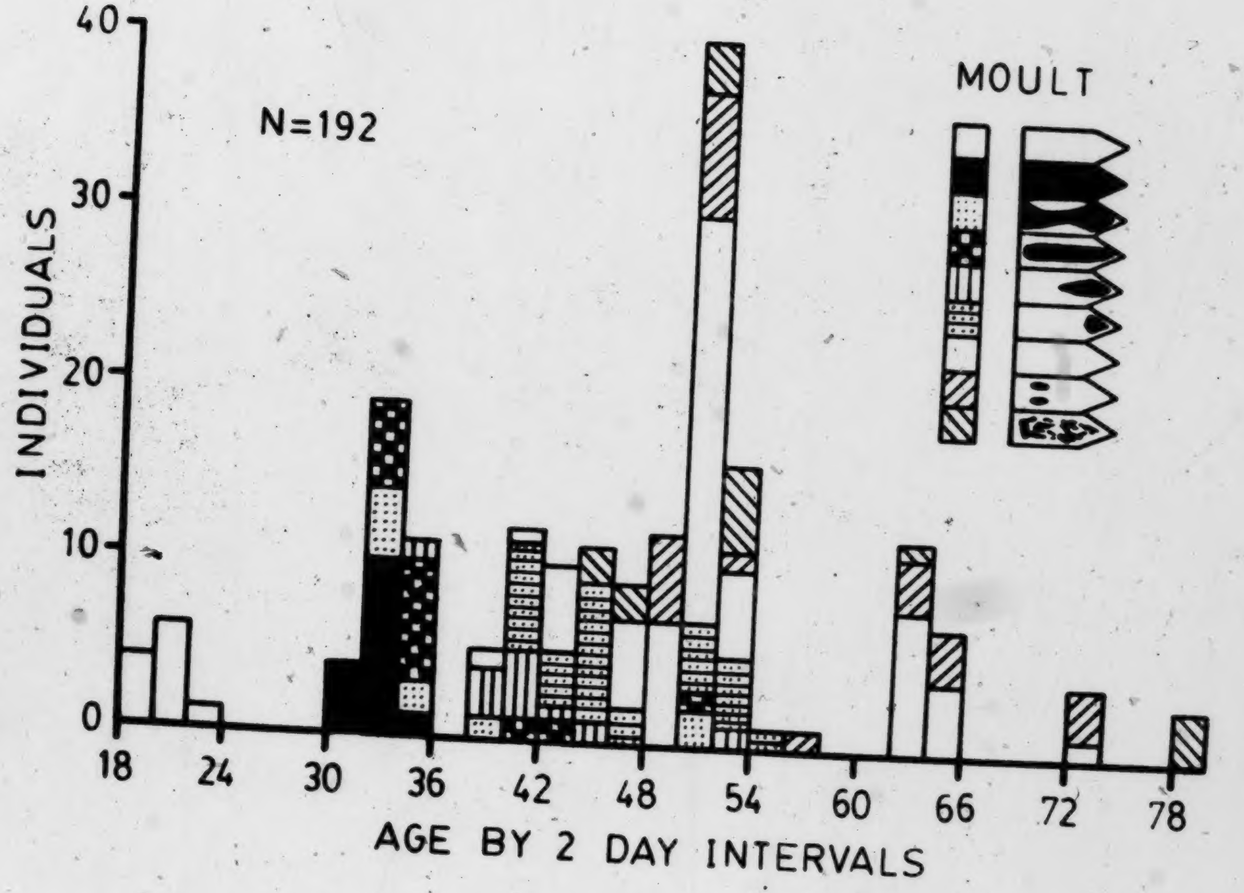

Figure 4. Moult pattern in animals of known age raised in outdoor pens.

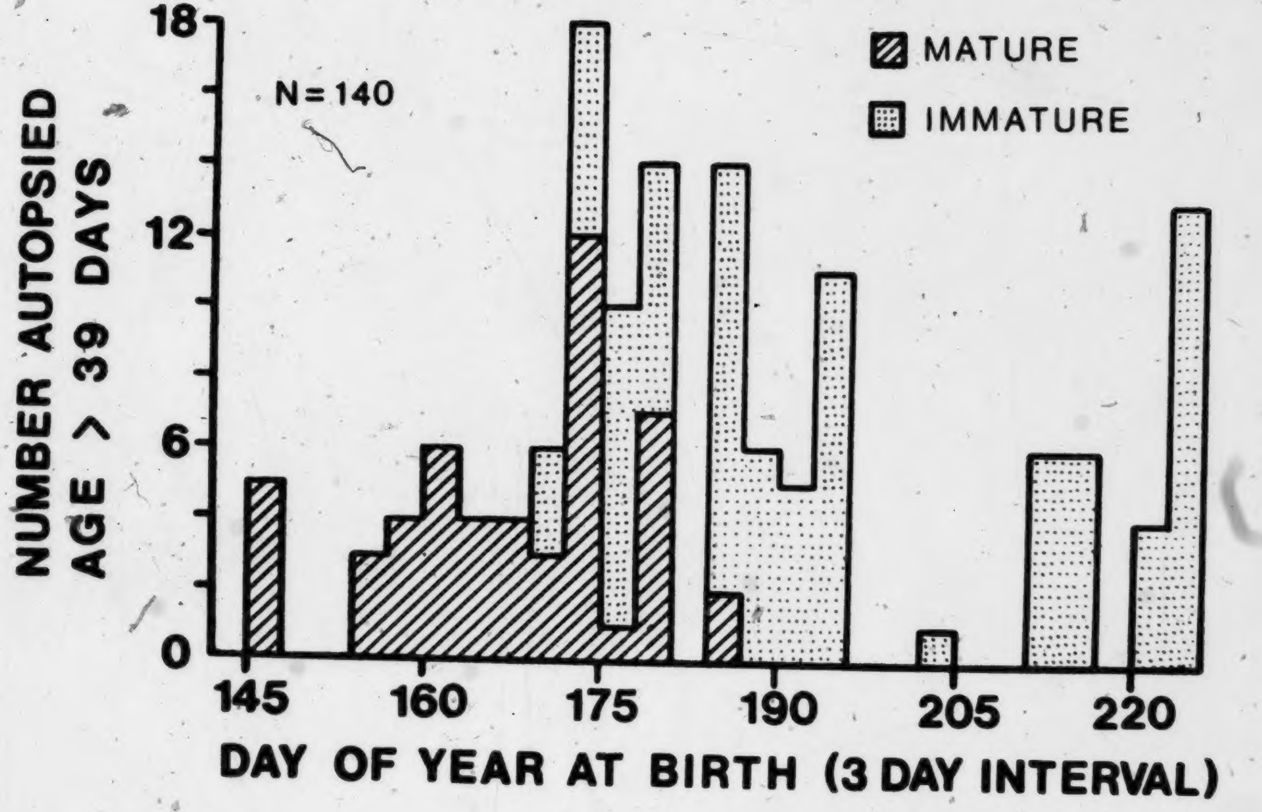

Figure 5. Attainment of sexual maturity in animals raised in outdoor pens.

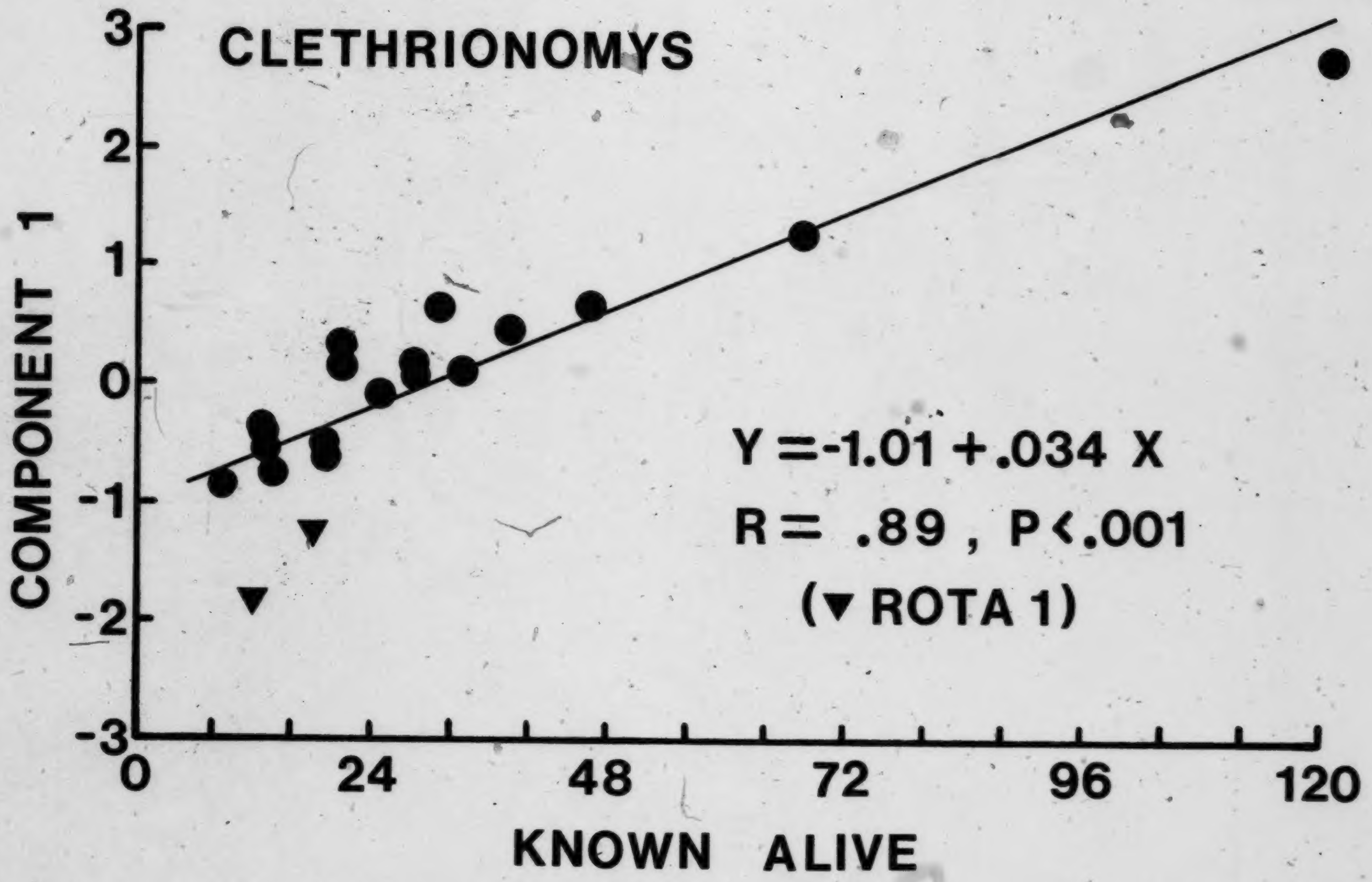

Figure 6. Relationship between a composite variable, calculated from a Principal Components Analysis of three indices of spatial behavior, and the number of animals known alive on the multiple capture grid in each rota of 1976 and 1977.

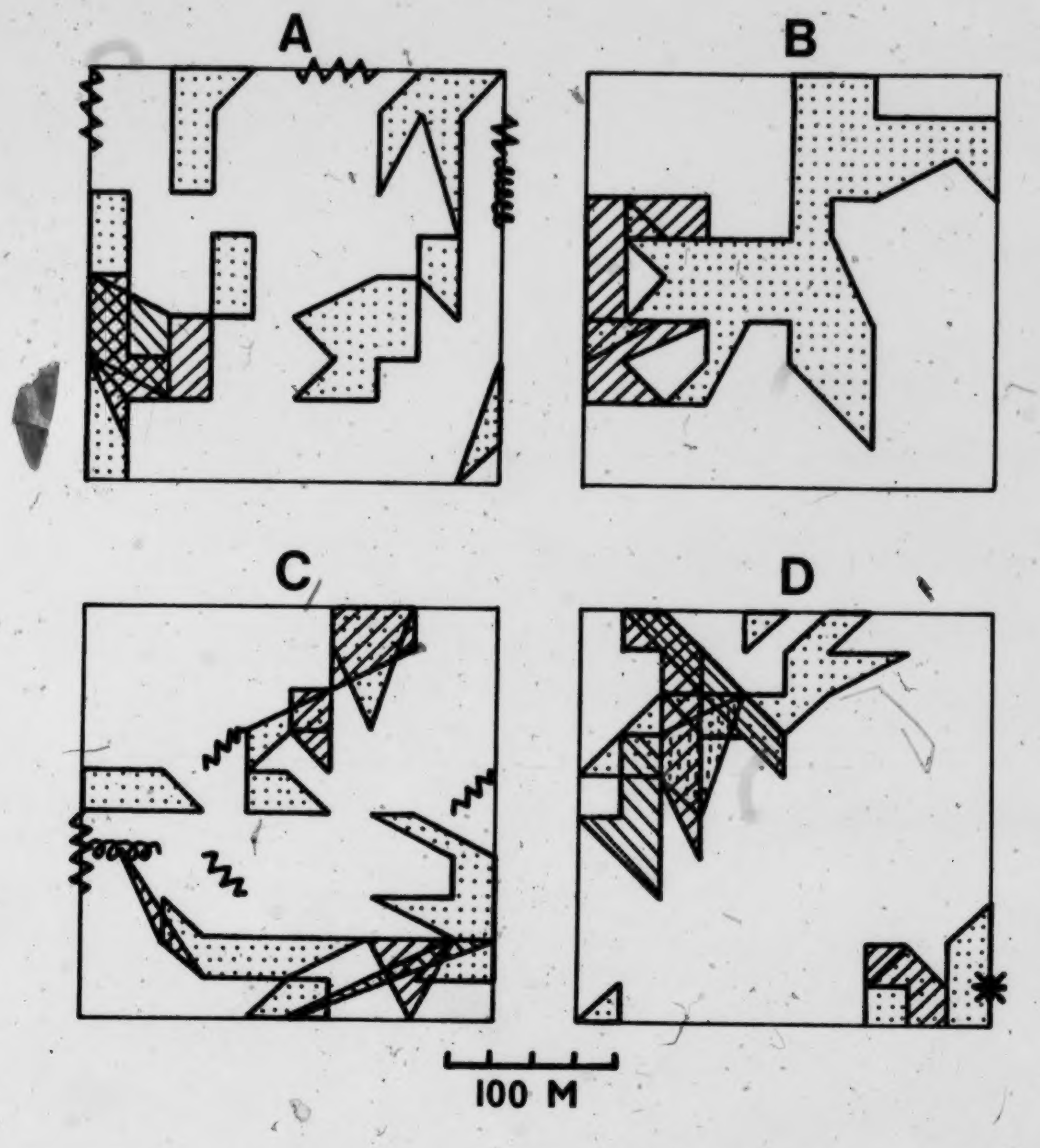

Figure 7. Minimum Area Home Ranges of animals caught on the multiple capture grid in at least two rotas from rota 5 on in 1976 (A: Mature females, B: Overwintered males, C: Immature females, D: Young mature males), (Animals caught at one point are represented by an asterisk, animals caught at two or more points in a line are represented by a squiggle, shading is used to differentiate animals).

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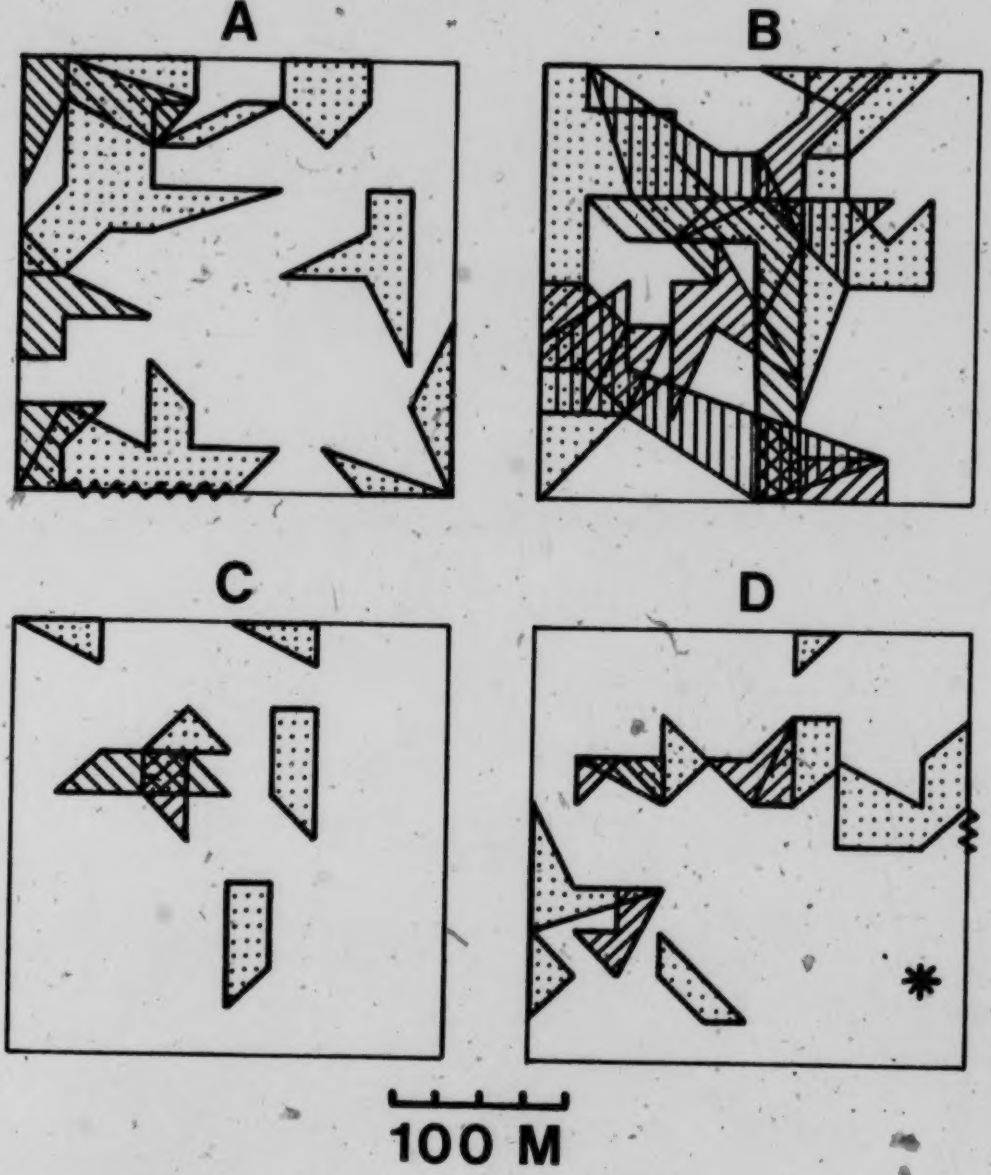

Figure 8. Minimum Area Home Ranges of all animals caught on the multiple capture grid in at least two rotas from rota 5 on in 1977 (A: Mature females, B: Mature males, C: Immature females, D: Immature males), (symbols as in Fig. 7).

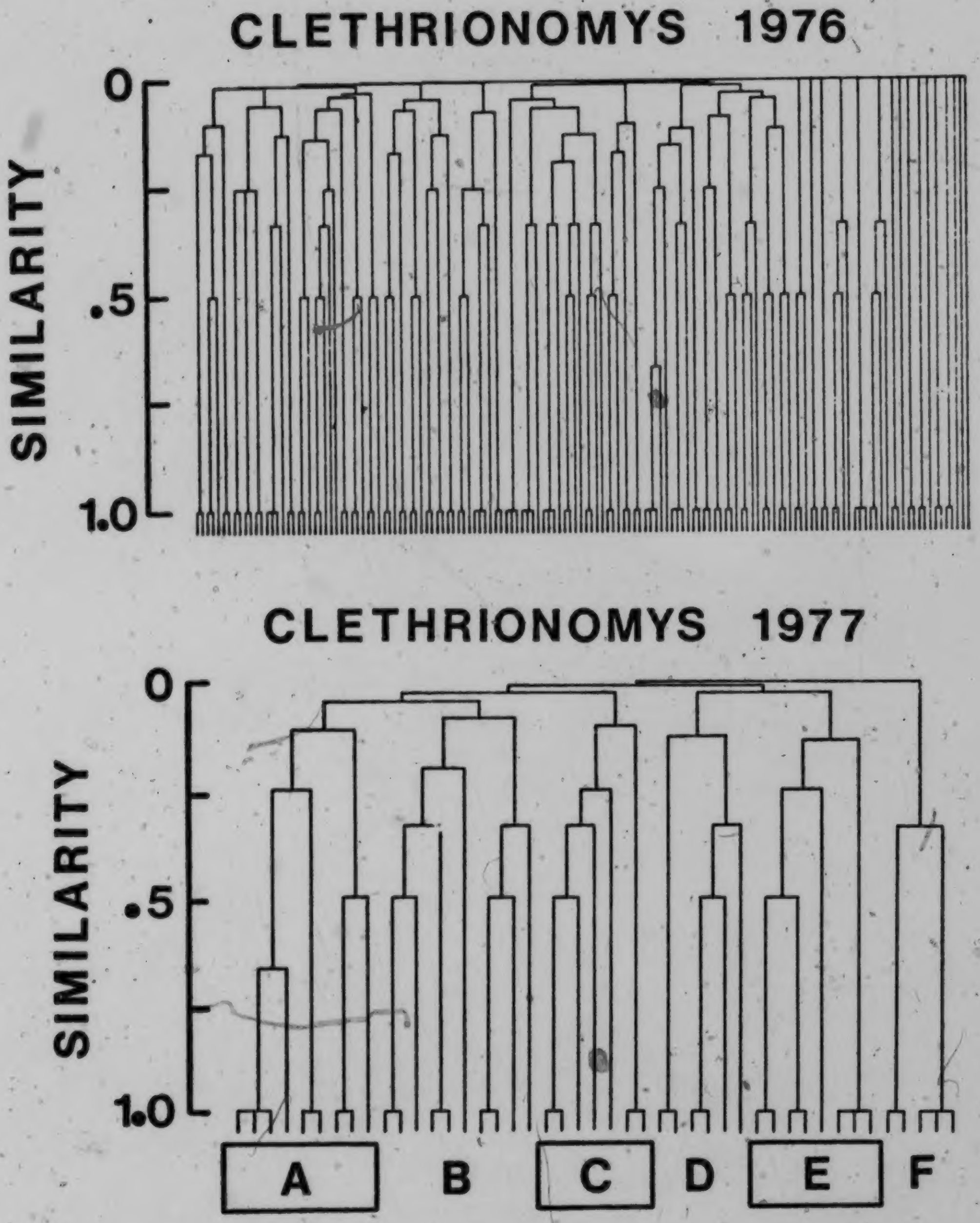

Figure 9. UPGMA cluster analysis of matrices of behavioral similarity generated from multiple capture data in 1976 and 1977.

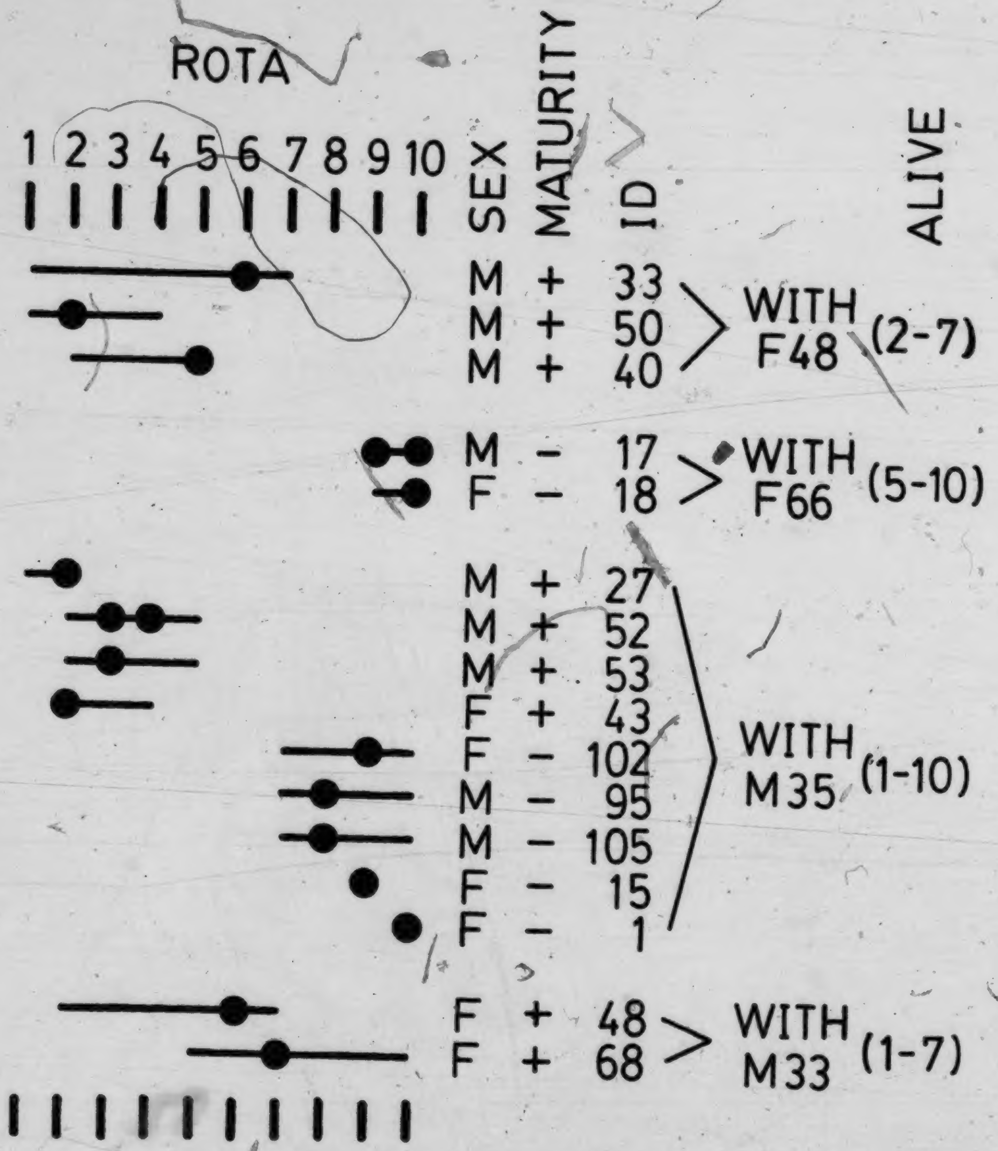

Figure 10. Schematic representation of the multiple capture histories of four long-lived mature voles in 1976 (see text for explanation).

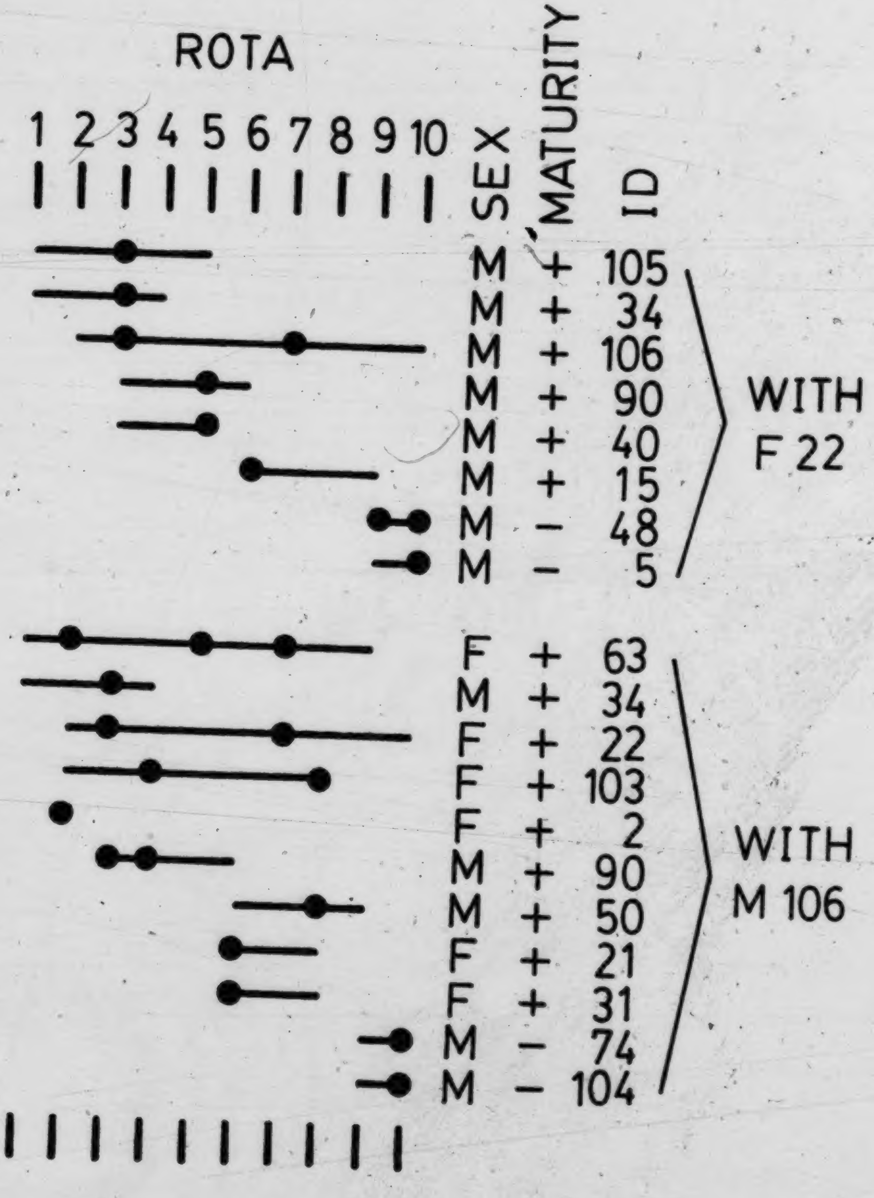

Figure 11. Schematic representation of the multiple capture histories of two long-lived mature voles in 1977 (see text for explanation).

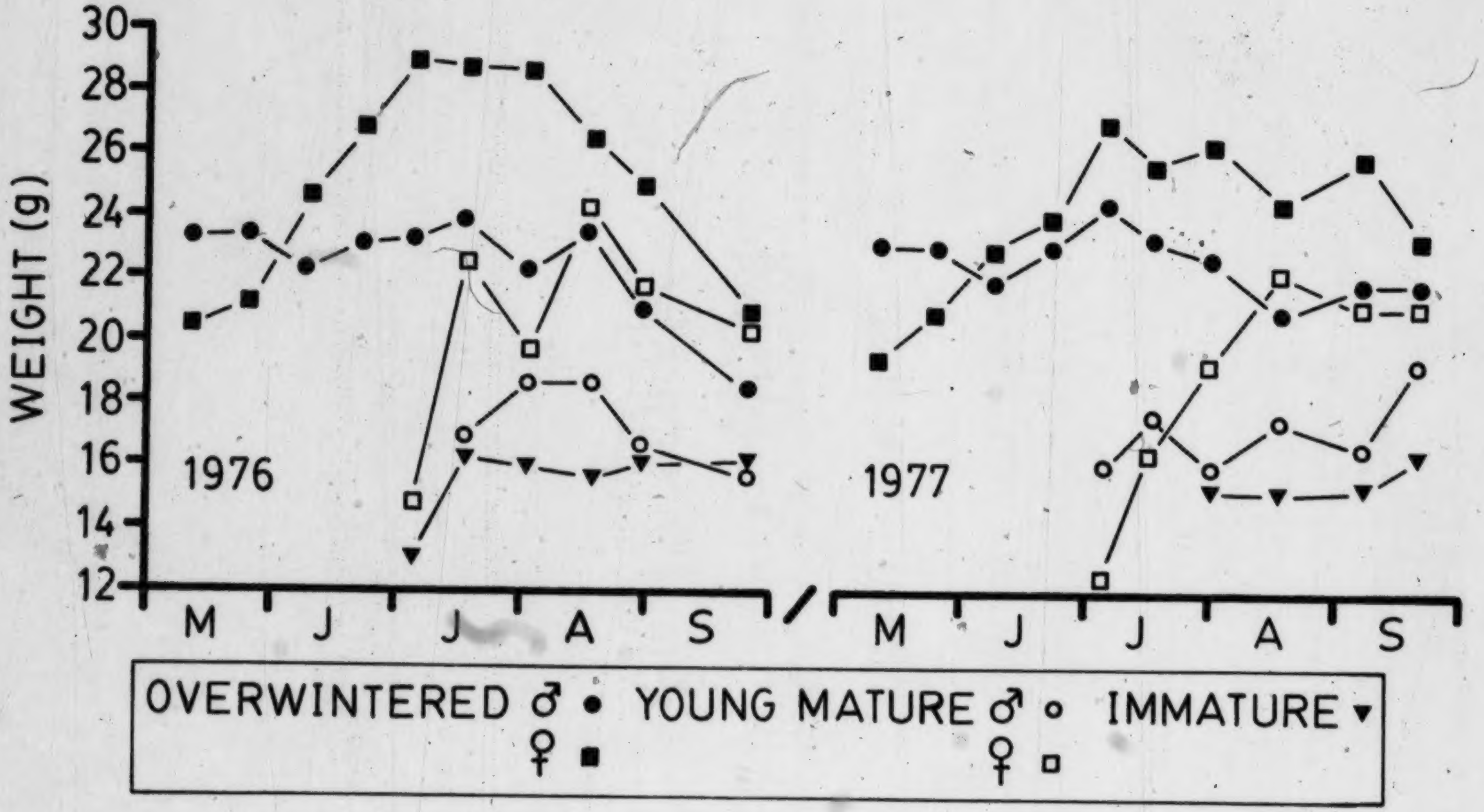

Figure 12. Mean weights of animals captured on the multiple capture grid.

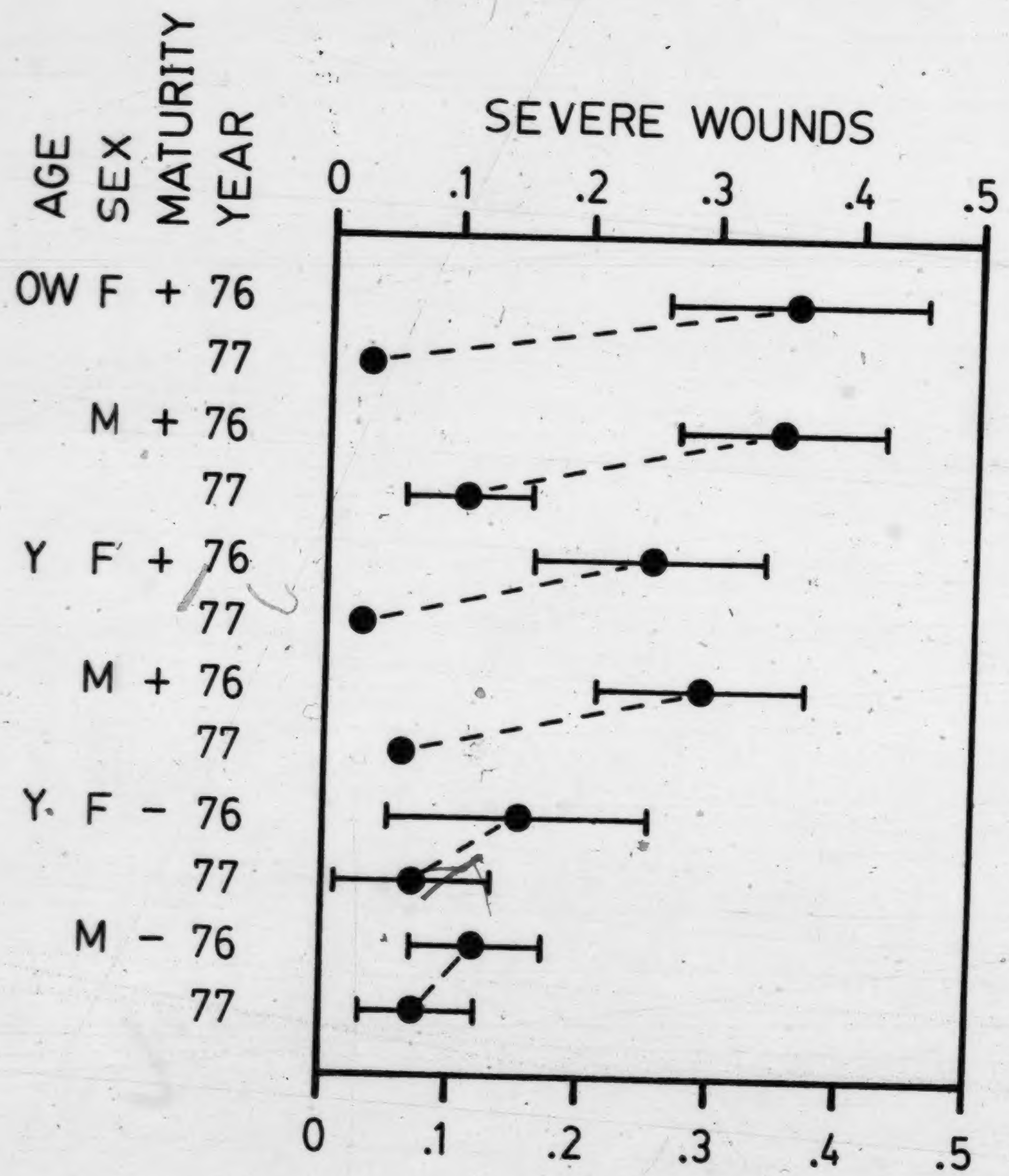

Figure 13. Proportion of pelts with severe wounds in Clethrionomys gapperi caught in the Heart Lake area in 1976 and 1977 (mean, 95% CI based on binomial distribution).

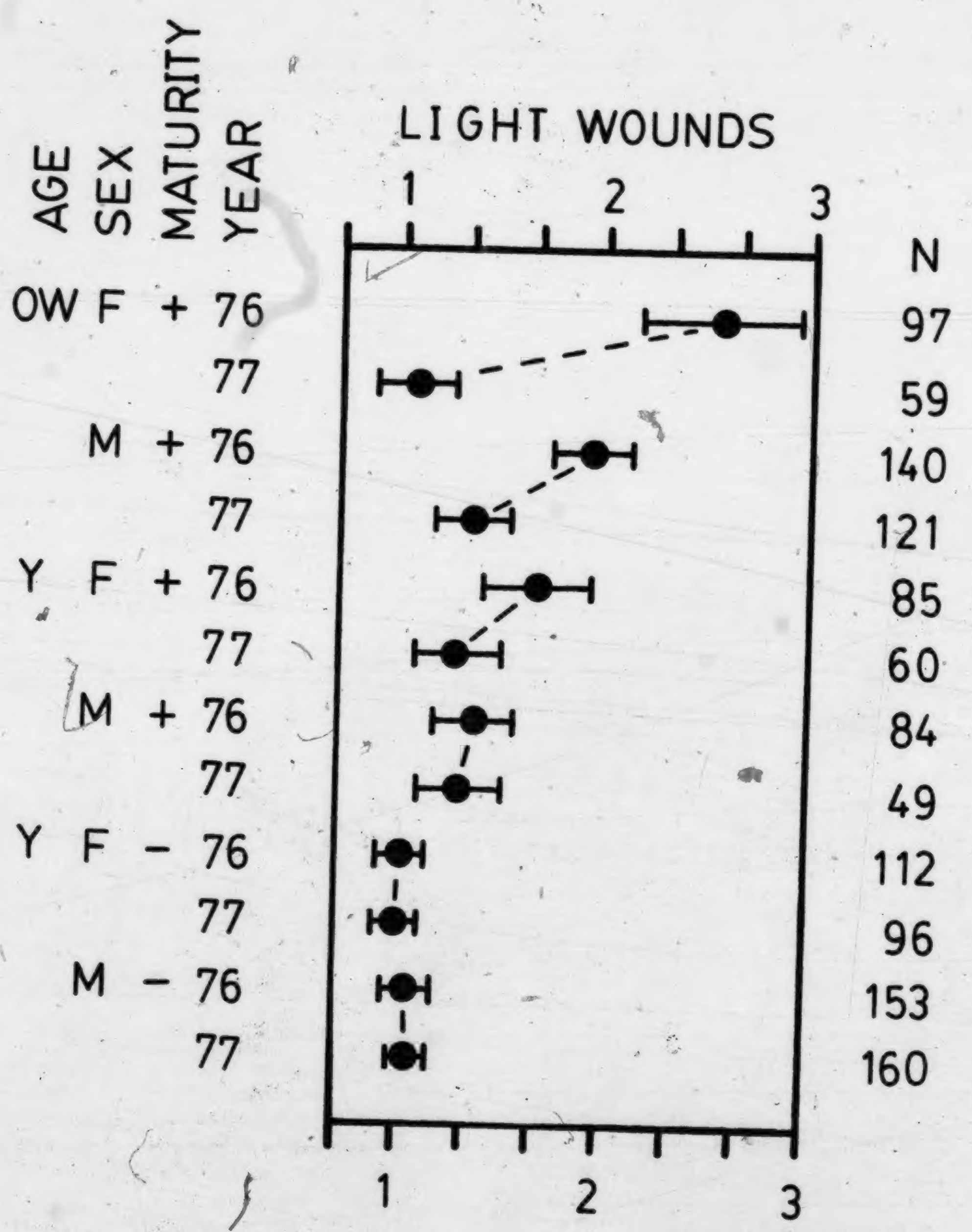

Figure 14. Number of light wounds (square root transformed data) recorded from pelts of *Clethrionomys gapperi* caught in the Heart Lake area in 1976 and 1977 (mean, 95% CI).

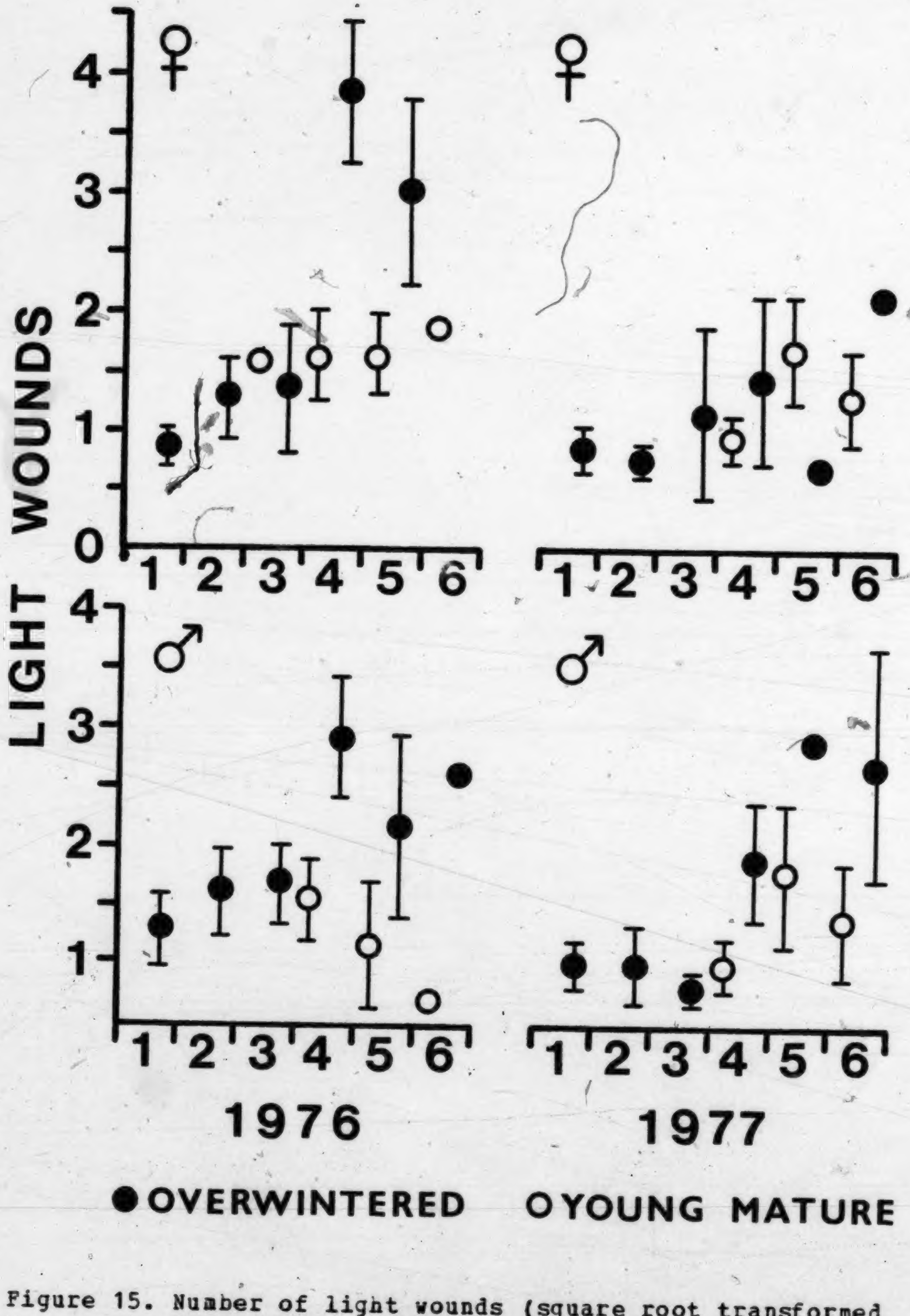

Figure 15. Number of light wounds (square root transformed data) by time periods in mature voles (mean, 95% CI, N < 6 represented by a dot).

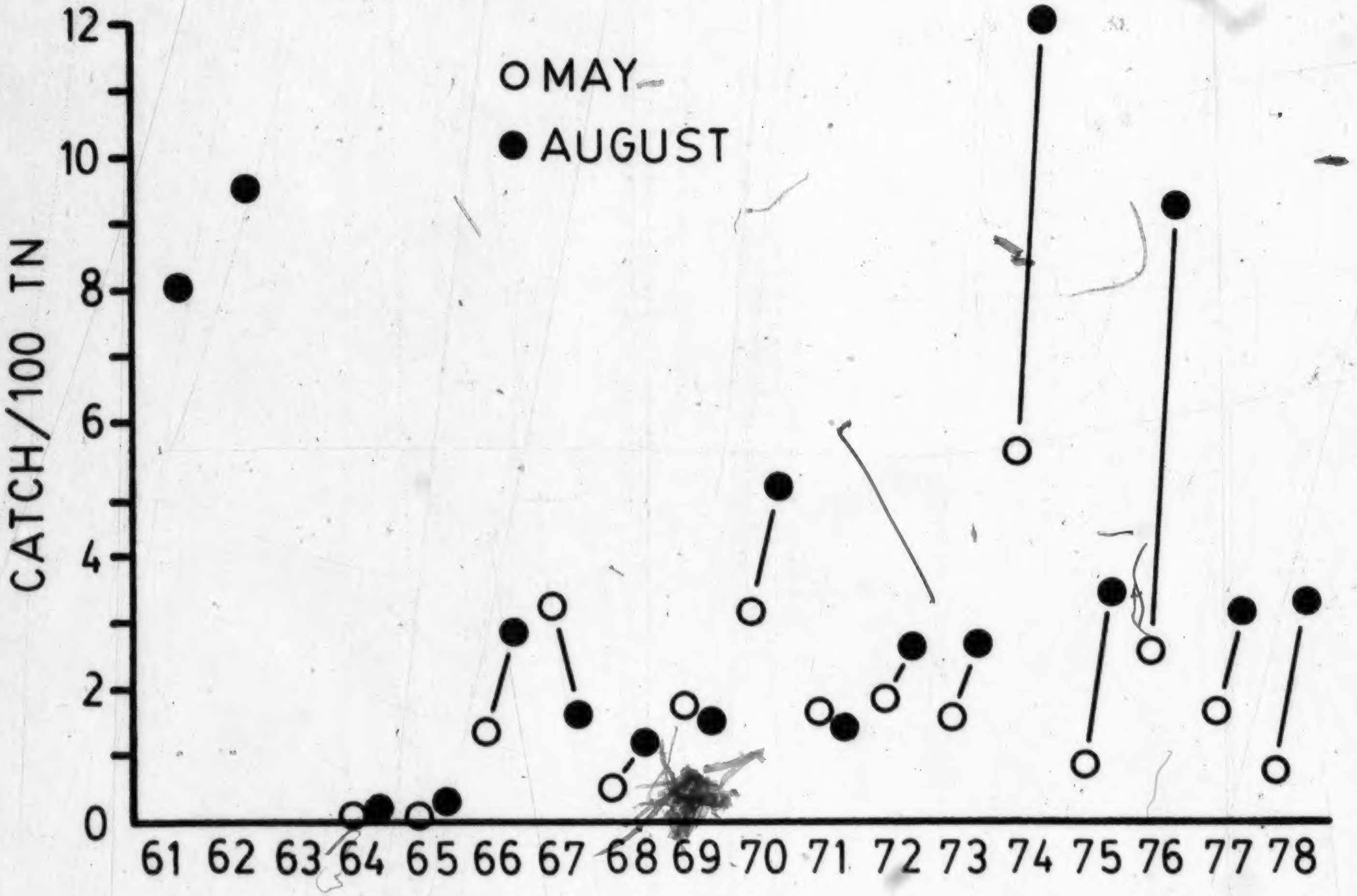

Figure 16. Snap-trap indices of population density for *Clethrionomys gapperi* at Heart Lake, N.W.T. (Fuller 1969, 1977a, unpublished).

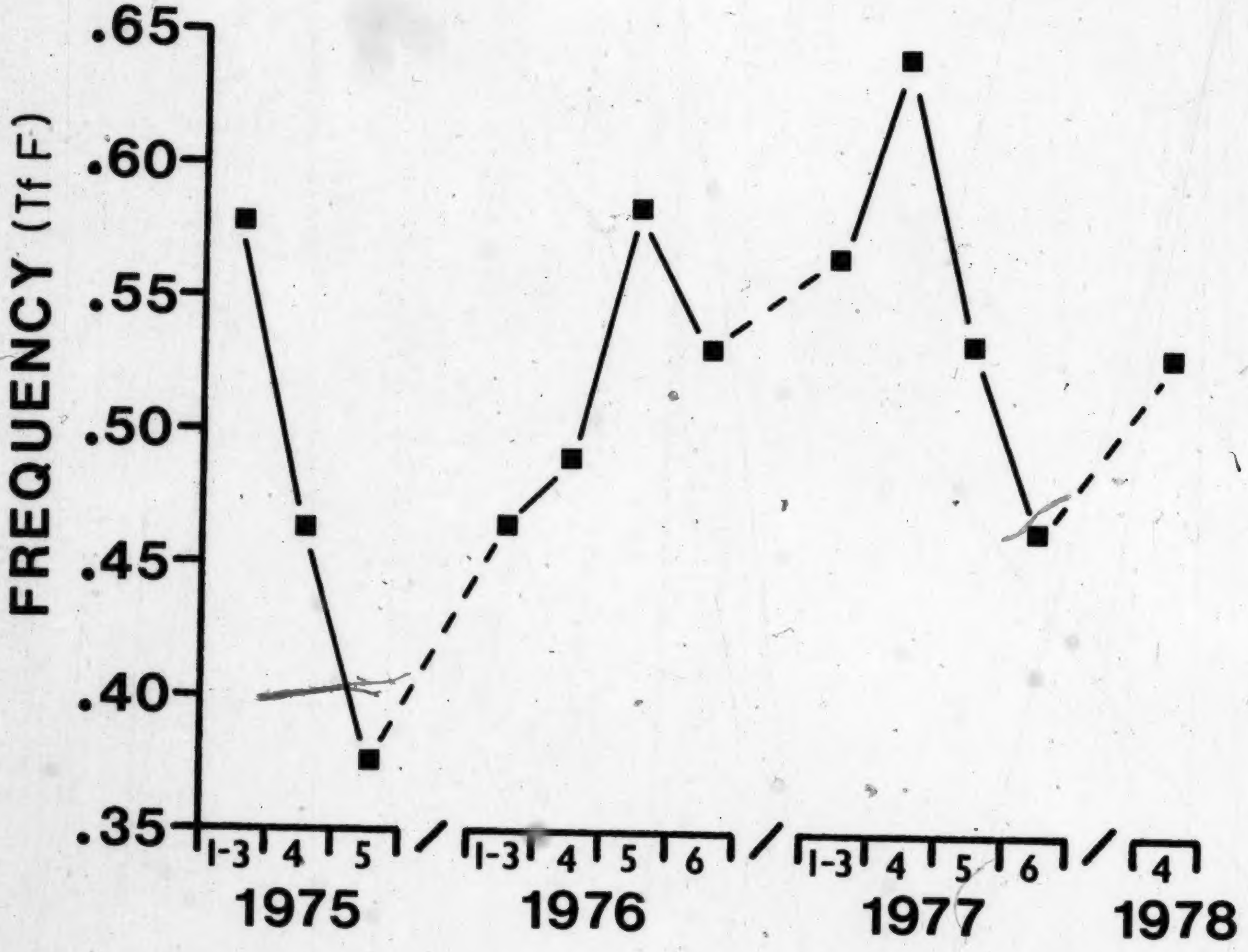

Figure 17. Frequency of the fast transferrin allele by time periods from 1975 to 1978 in all Clethrionomys gapperi caught at Heart Lake, N.W.T.

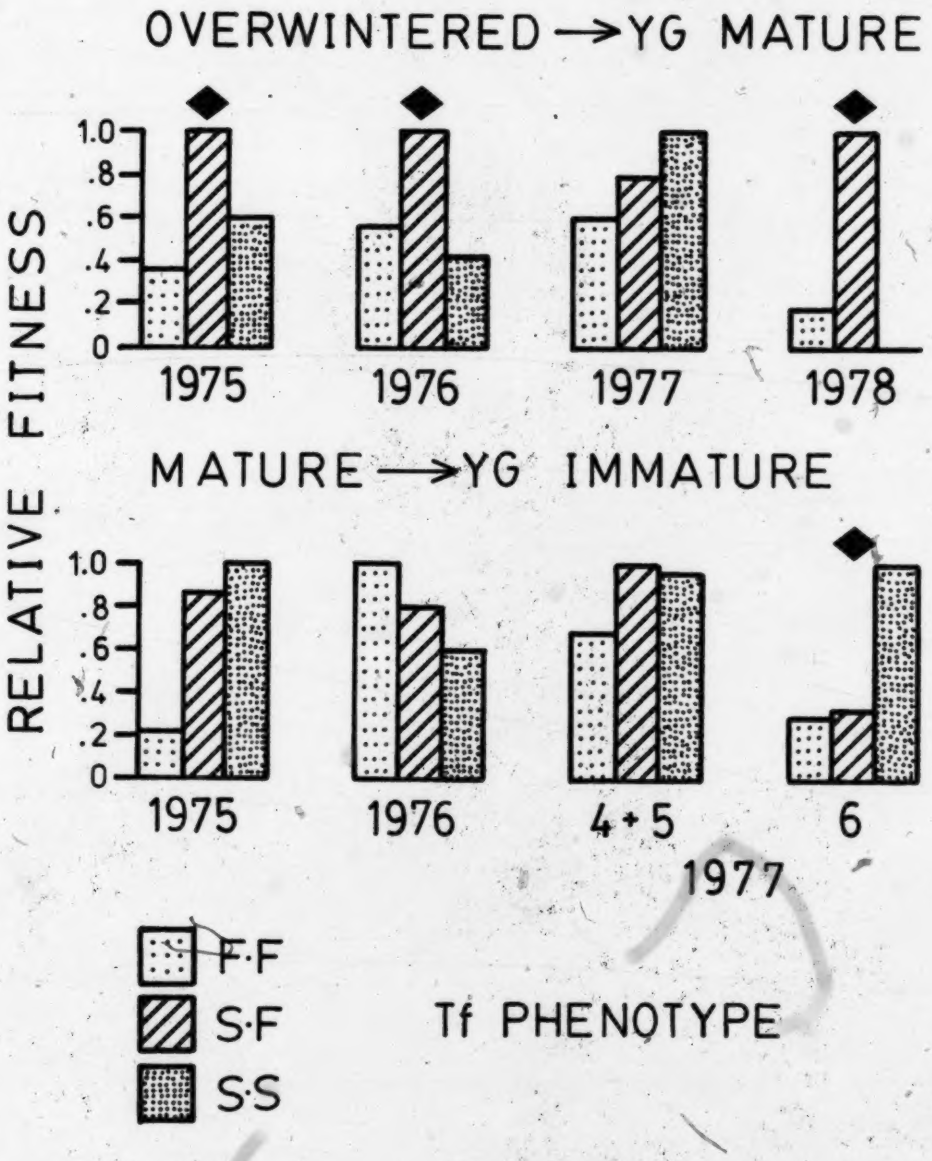

Figure 18. Relative "fitness" at the transferrin locus of the early-summer mature generation born to overwintered animals, and the mid and late-summer generation born to overwintered and young mature animals (diamonds refer to significant differences between observed phenotypic frequencies of young and those expected from random mating in the parental generation).

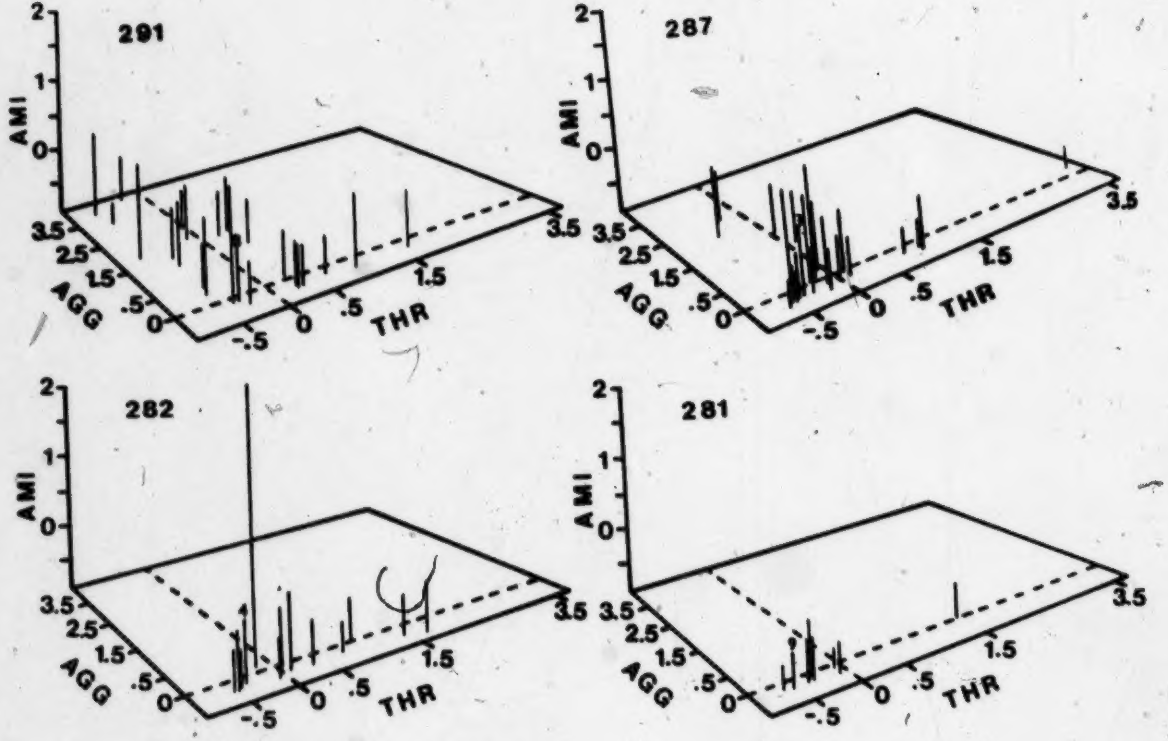

Figure 19. Behavioral profiles of four individual overwintered males maintained in captivity and paired with various opponents of the same sex from May to September of 1977.

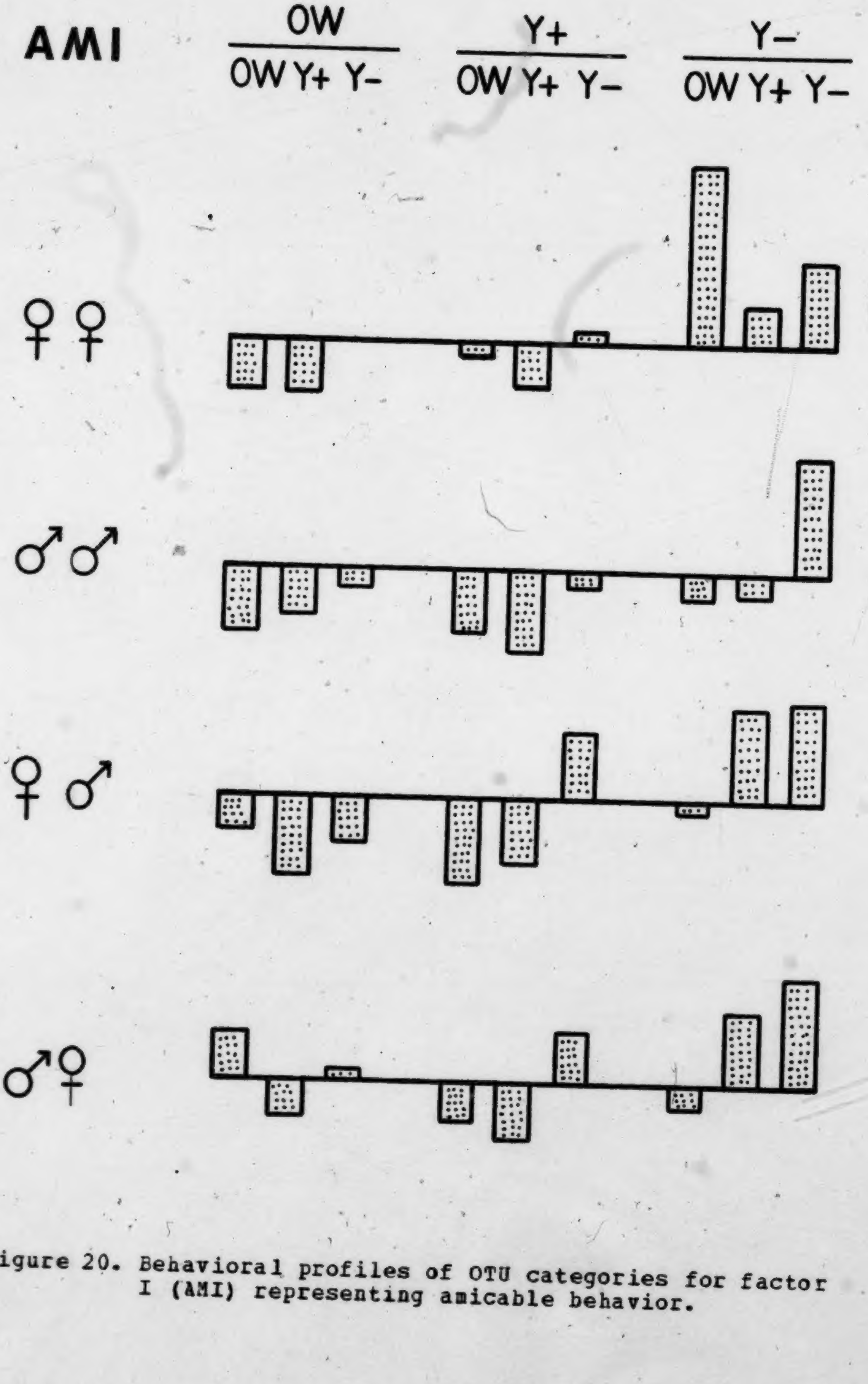

Figure 20. Behavioral profiles of OTU categories for factor I (AMI) representing amicable behavior.

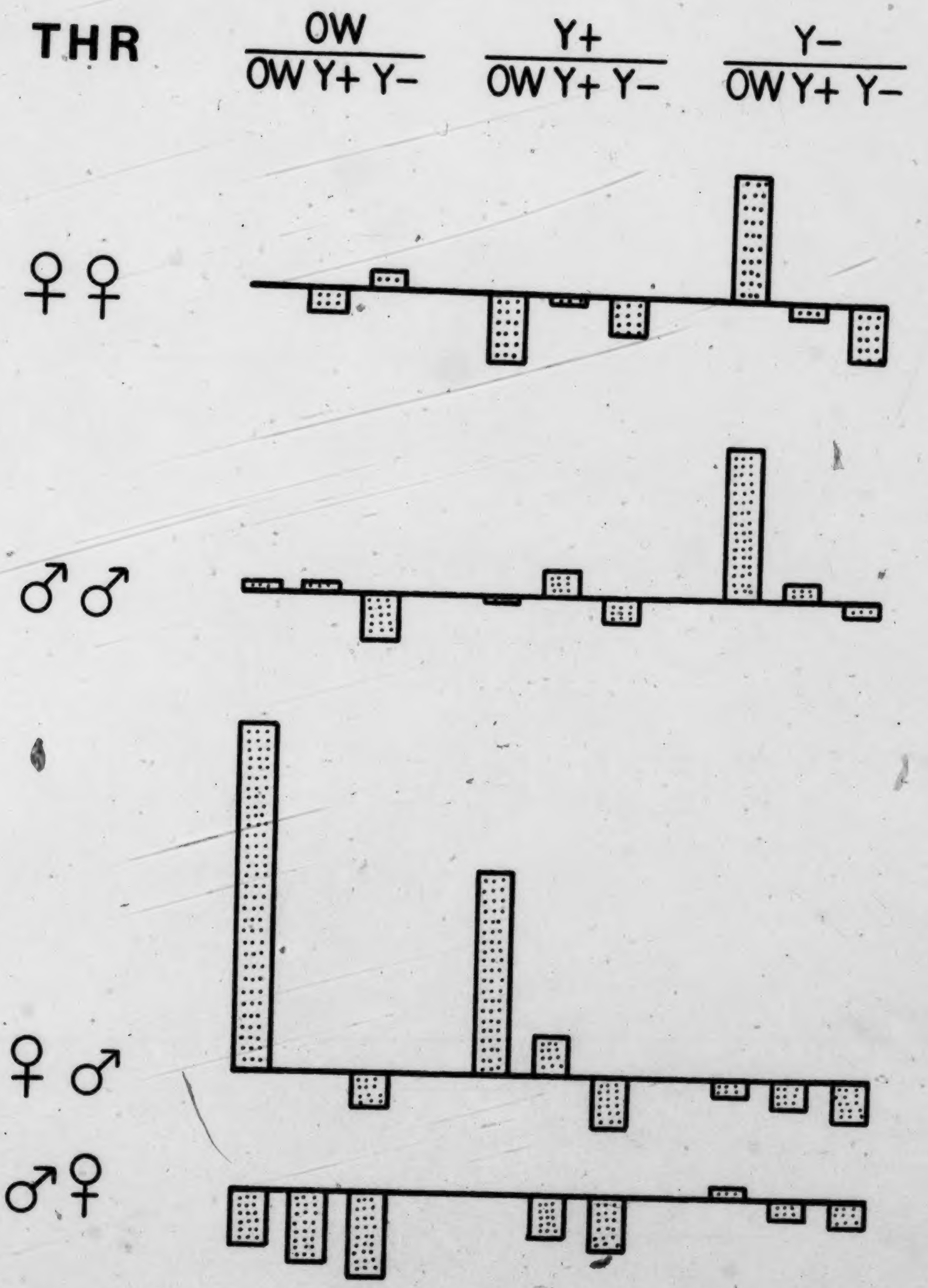

Figure 21. Behavioral profiles of OTU categories for factor II (THR) representing threat behavior.

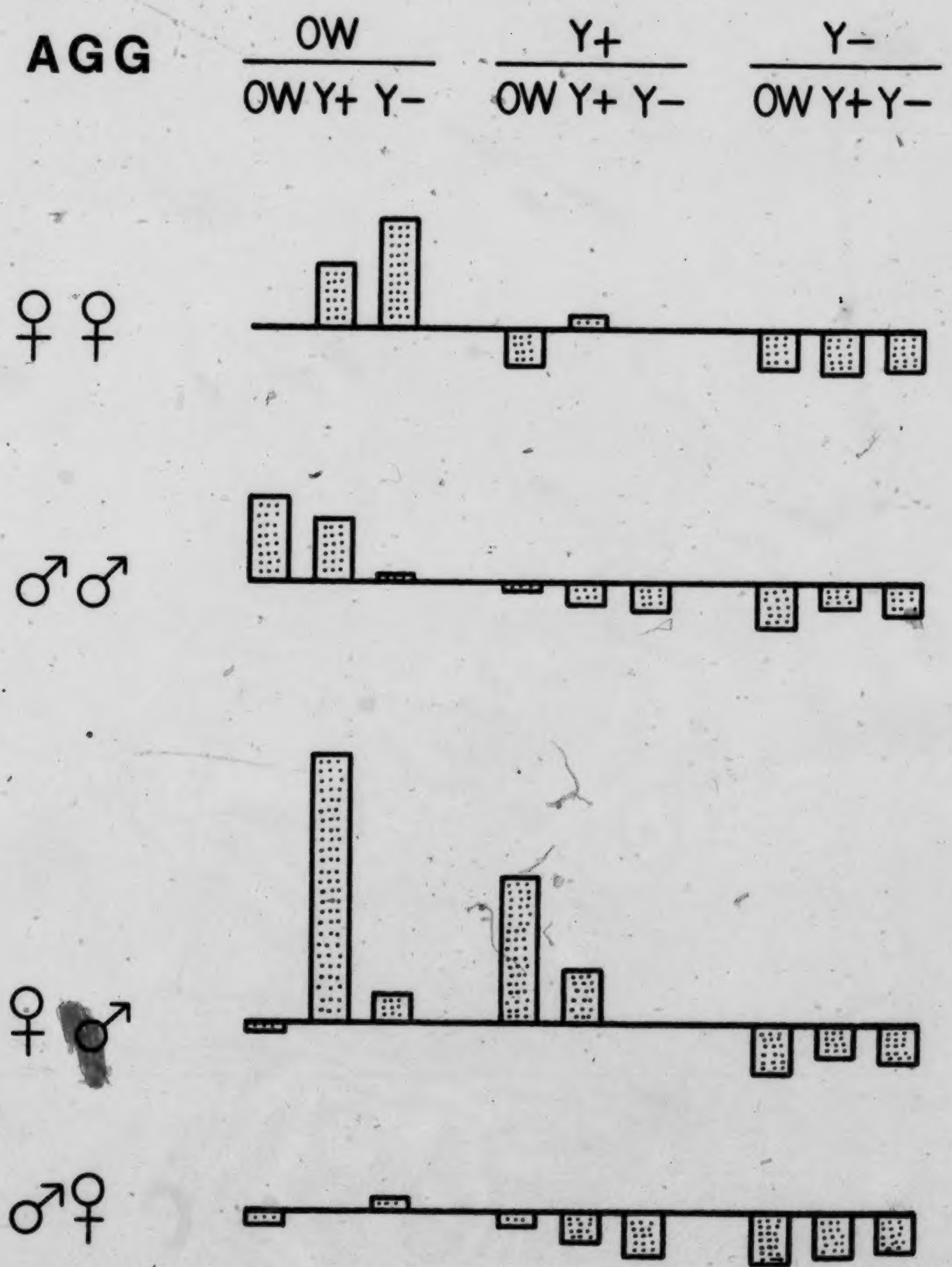

Figure 22. Behavioral profiles of OTU categories for factor III (AGG) representing attack behavior.

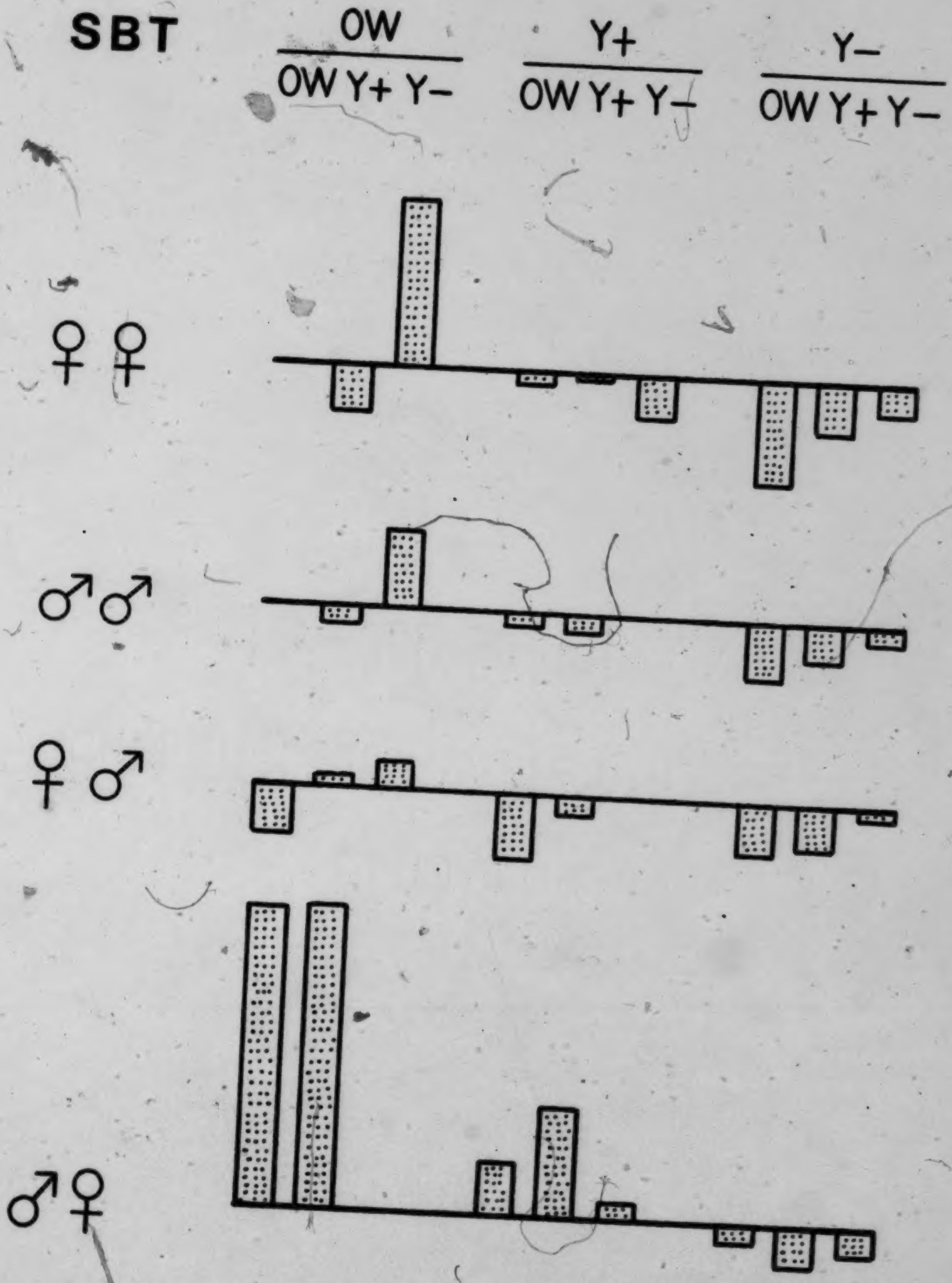

Figure 23. Behavioral profiles of OTU categories for factor IV (SBT) representing subordinate behavior.

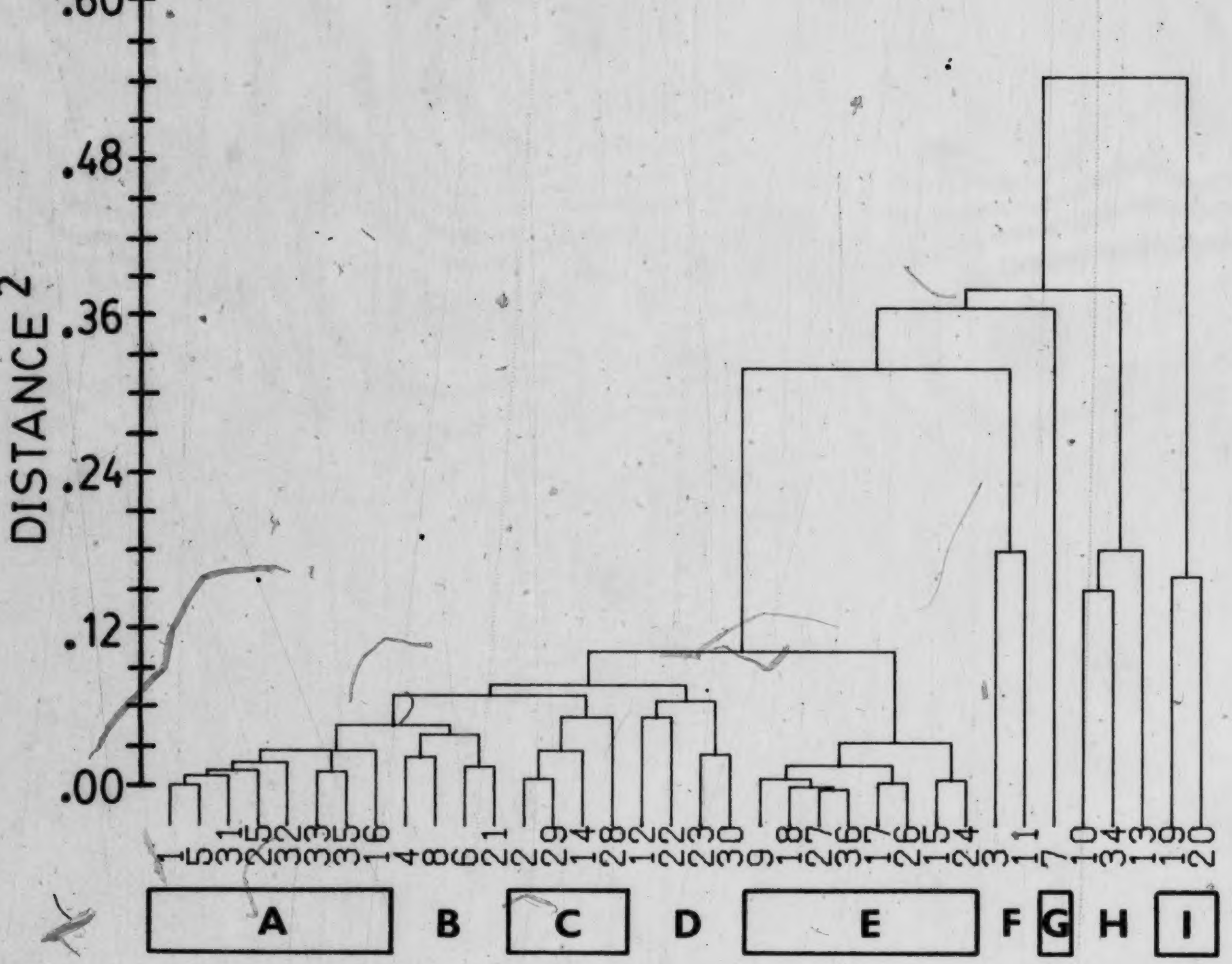

Figure 24. UPGMA analysis of behavior in sex, age and maturity categories (see Appendix 10-13 for correspondence of categories with ID numbers).

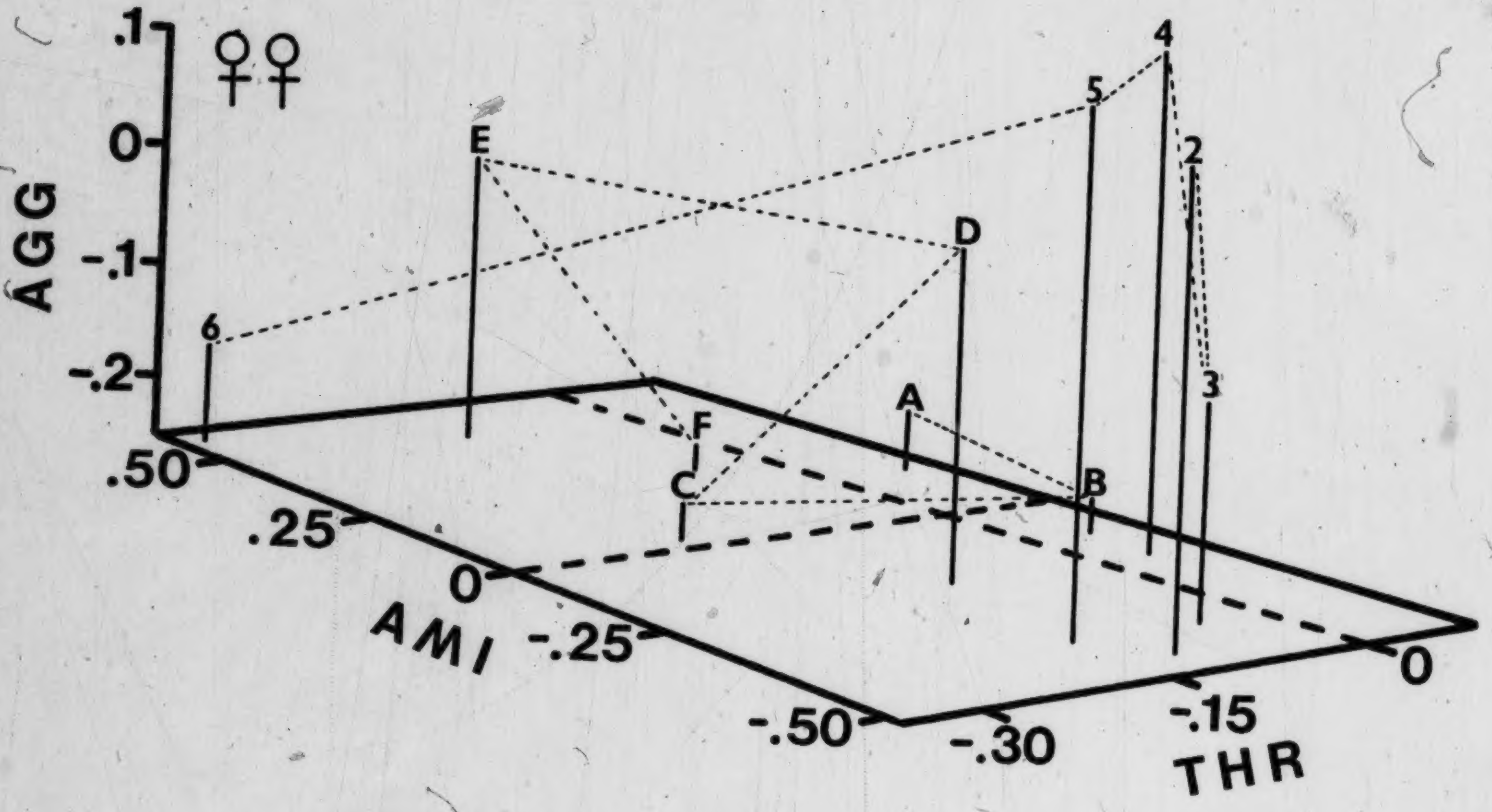

Figure 25. Mean scores on the first three factors in female-female trials by time periods (2 to 6: 1976, A to F: periods 1 to 6 of 1977).

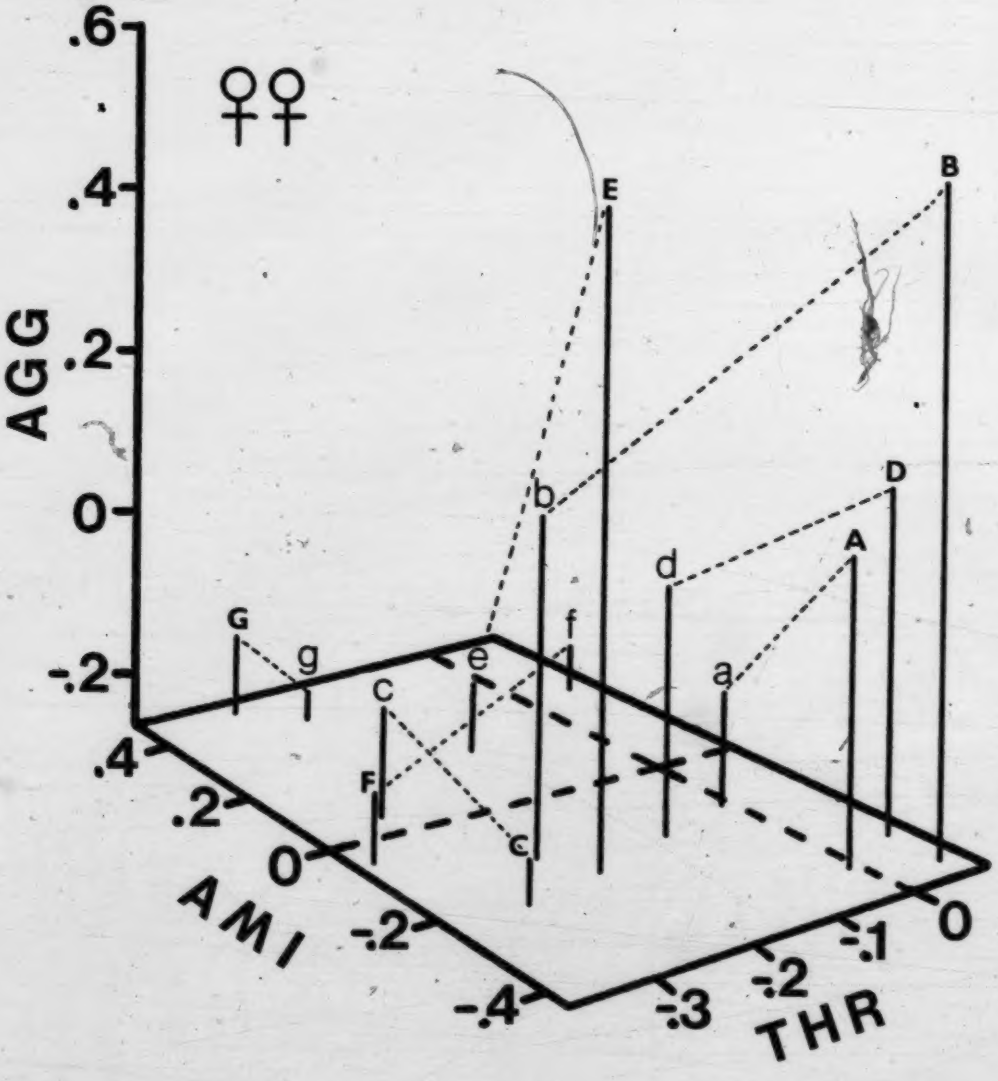

Figure 26. Mean scores on the first three factors in female-female trials broken down by age and maturity categories in each year (upper case: 1976, lower case: 1977, A: OW vs OW, B: OW vs Y+, C: Y+ vs OW, D: Y+ vs Y+, E: Y+ vs Y-, F: Y- vs Y+, G: Y- vs Y-).

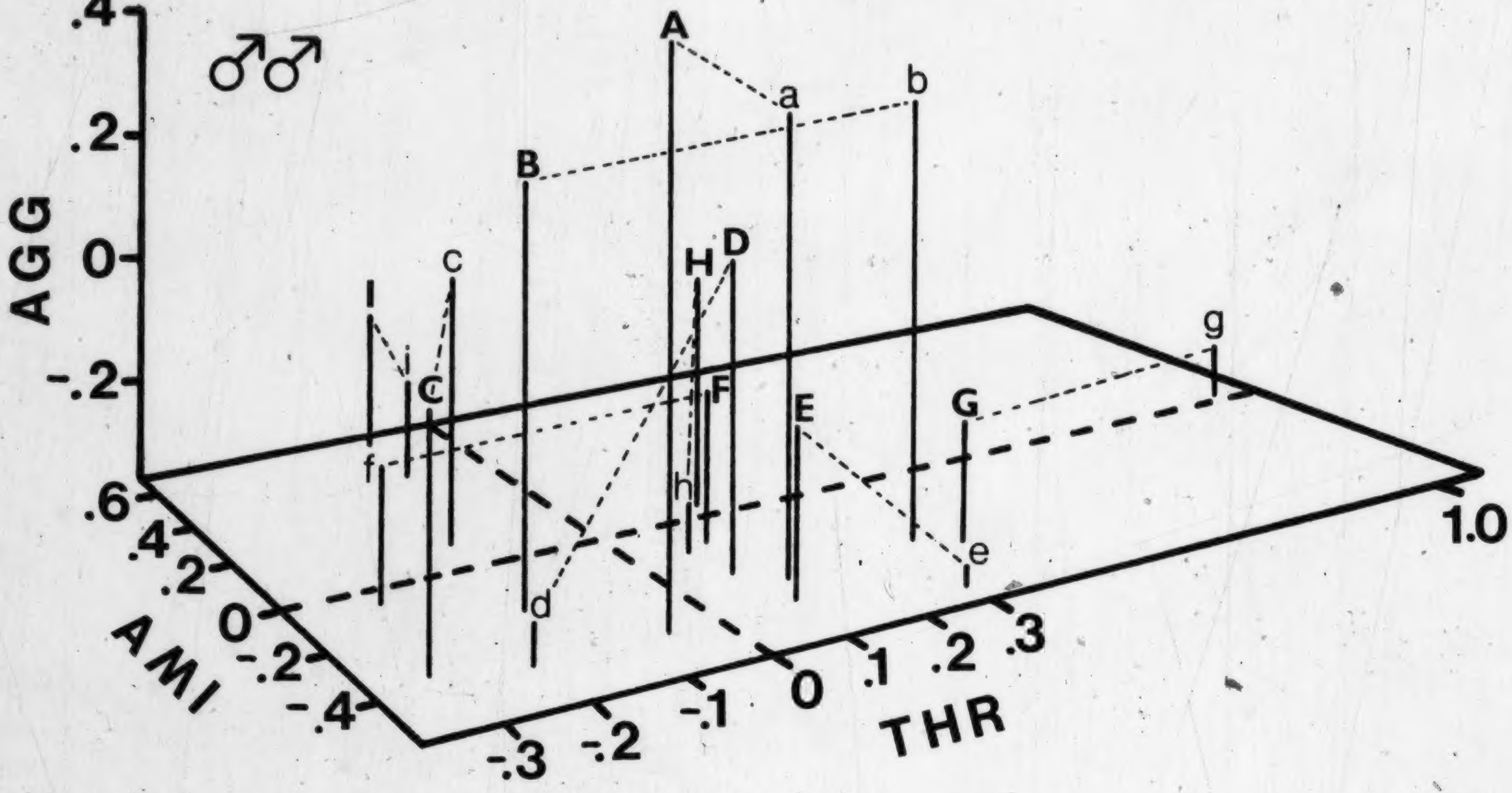

Figure 27. Mean scores on the first three factors in male-male trials broken down by age and maturity categories in each year (upper case: 1976, lower case: 1977, A: OW vs OW, B: OW vs Y+, C: OW vs Y-, D: Y+ vs OW, E: Y+ vs Y+, F: Y+ vs Y-, G: Y- vs OW, H: Y- vs Y+, I: Y- vs Y-).

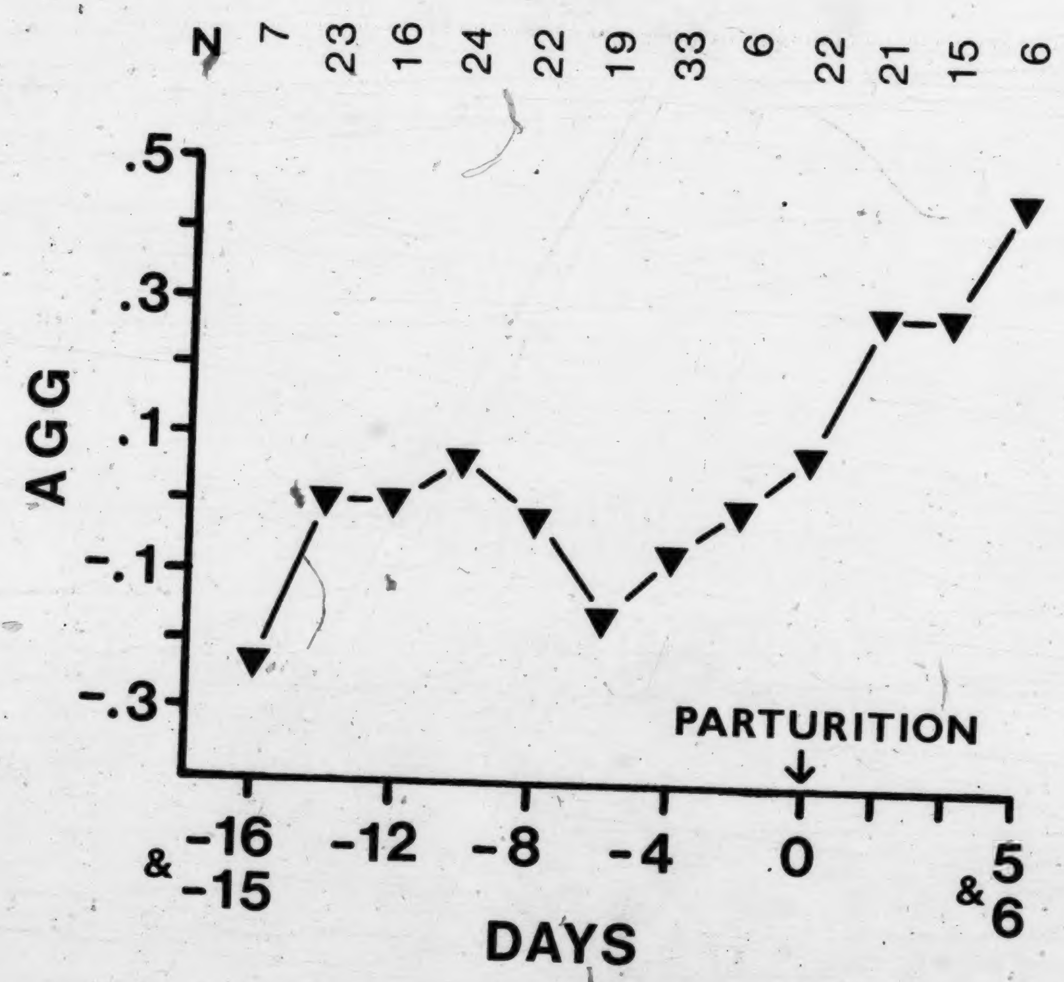

Figure 28 Mean scores on the attack factor (AGG) in trials between mature females relative to the day of parturition.

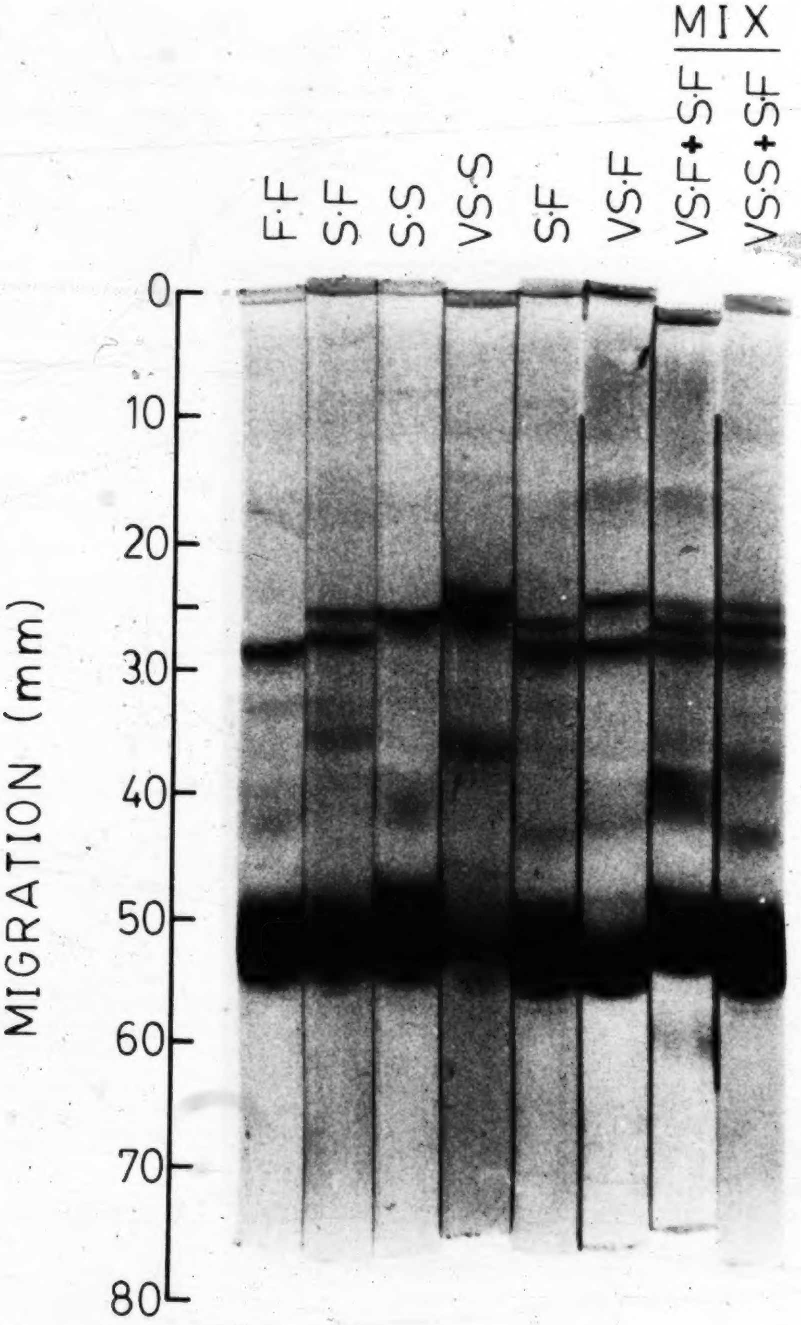
MIX
F·F
S·F
S·S
VS·S
S·F
VS·F
VS·F+S·F
VS·S+S·F
MIGRATION (mm)
0
10
20
30
40
50
60
70
80

Plate 1. Polyacrylamide gels stained with Nitroso R salt solution showing the different transferrin types (VS=very slow, S=slow, F=fast).

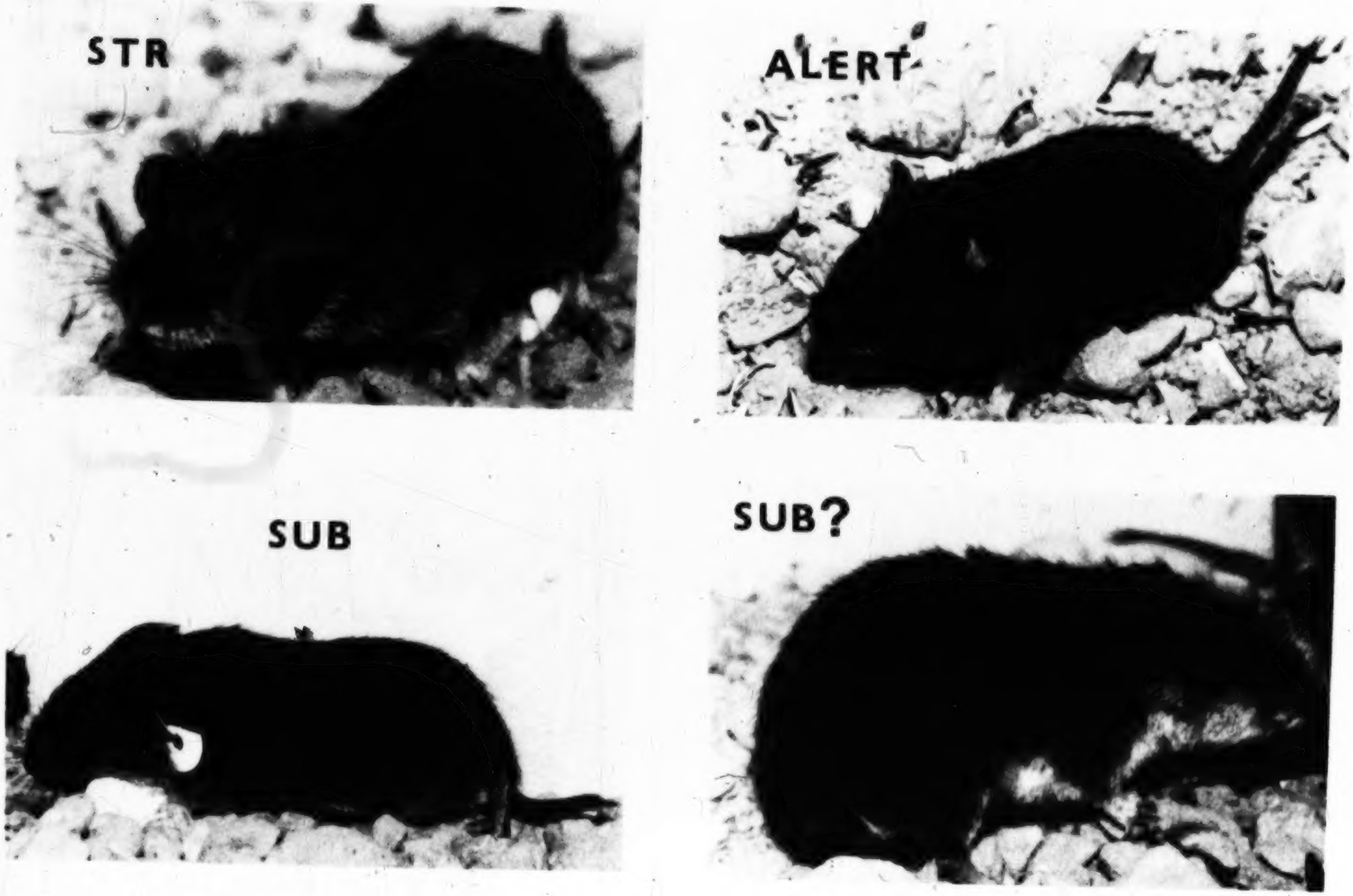
STR
ALERT
SUB
SUB?

Plate 2. Stretch (STR), alert (ALERT), and submissive (SUB) postures of *Clethrionomys gapperi*.

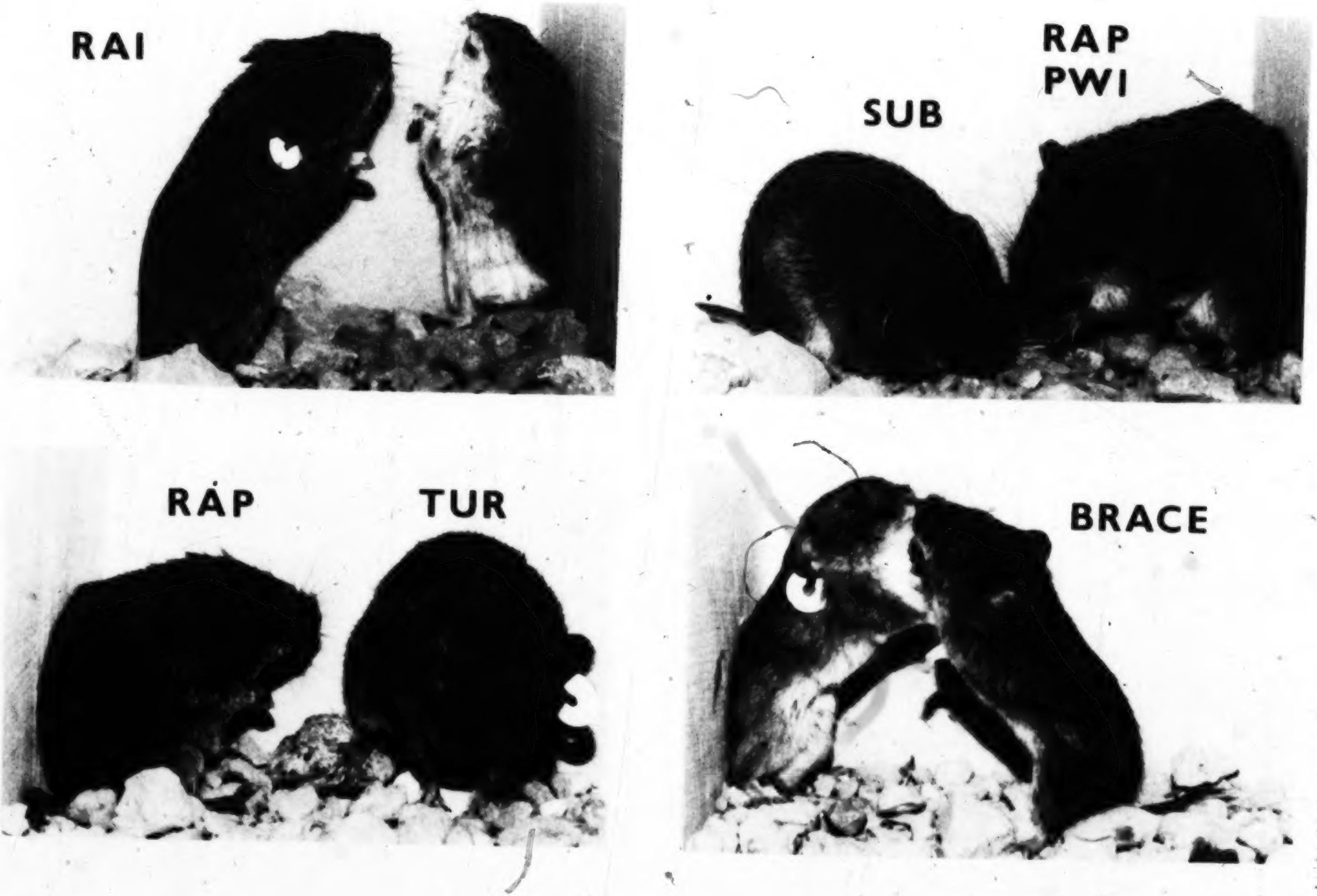
RAI
SUB
RAP
PWI
RAP
TUR
BRACE

Plate 3. Raise (RAI), raise partially (RAP), submissive (SUB), pawbeat 1 (PW1), turn away (TUR), and bracing (BRACE) postures of Clethrionomys gapperi.

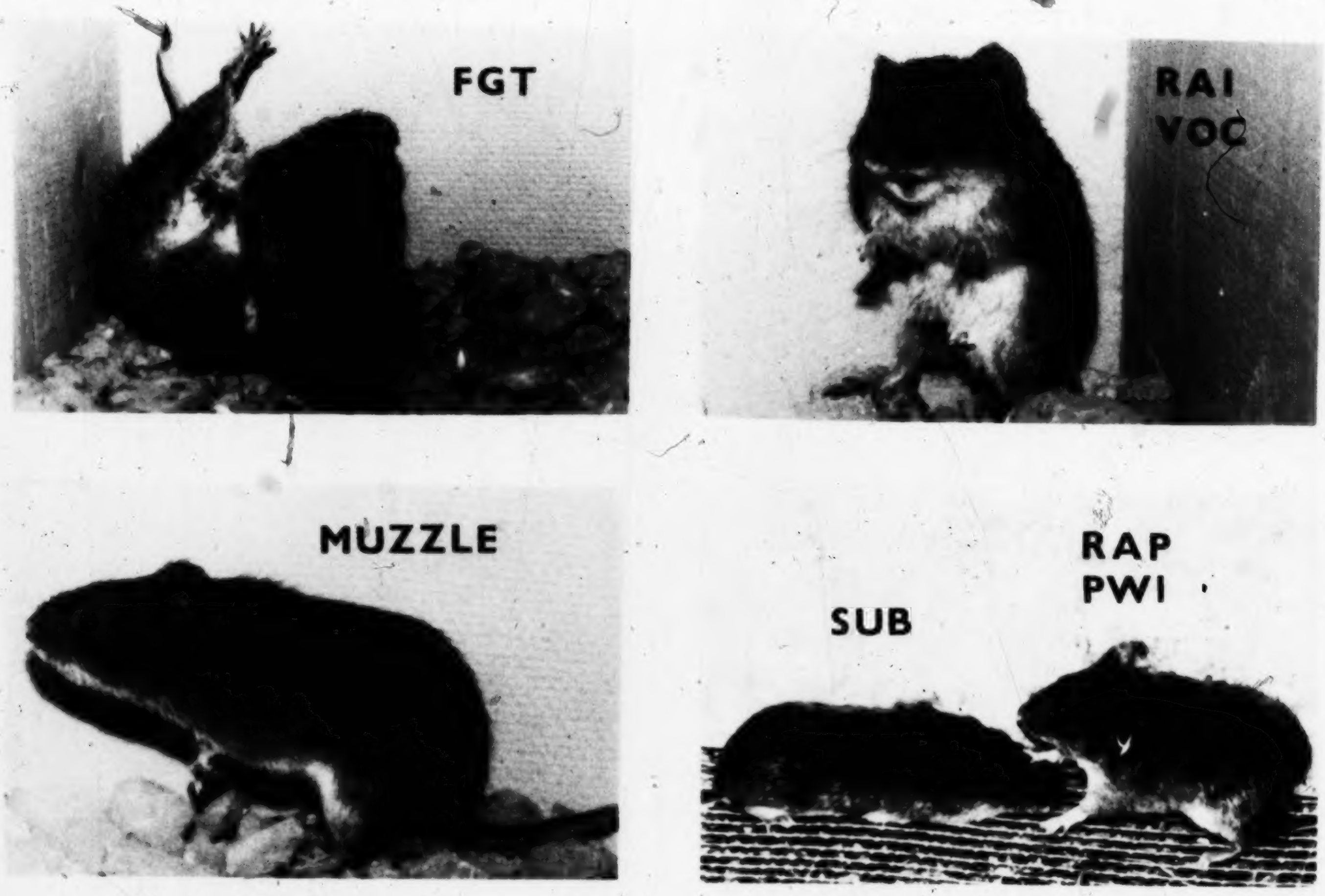
FGT
RAI
VOC
MUZZLE
RAP
PWI
SUB

Plate 4. Fighting (FGT), raise (RAI), squeal vocalization with open mouth display (VOC), muzzle control (MUZZLE), raise partially (RAP), pawbeat 1 (PW1), and submissive (SUB) postures in Clethrionomys gapperi.

Appendix 1. Estimates of the area sampled by the 6.25-ha multiple capture grid.

	1976			1977		
Rota	ARL†	Area	Population Density	ARL	Area	Population Density
1	190	19.3	0.93	182	18.7	0.59
2	190	19.3	1.09	180	18.5	0.81
3	190	19.3	1.09	180	18.5	0.81
4	192	19.6	0.97	174	18.0	0.72
5	165	17.2	1.63	171	17.7	0.79
6	153	16.3	2.03	143	15.5	1.23
7	147	15.8	2.41	138	15.0	1.26
8	141	15.3	3.01	135	14.8	1.69
9	138	15.1	4.44	130	14.5	1.94
10	135	14.8	8.18	129	14.4	2.15

Note: The ARL is calculated from the mean ARL of all animals caught more than five times in each year, and is weighted for the sex and age composition of the population.

The area sampled is calculated by adding a boundary strip equal to 1/2 the ARL.

† ARL (Adjusted Range Length in meters), Area (ha), Density (animals known alive/ hectare).

Appendix 2. Regression equations between gross weight at capture and age at capture (estimated from M^2 tooth measurements), and between body length at autopsy and age at autopsy, in voles in the open and closed groove age-classes caught on Sherman traplines.

Sex	Maturity	Year	Intercept	Slope	DF	F	P	r^2
Gross weight (g) with Age (days)								
M	Immature	1976	13.0	0.083	67	13.44	0.00	0.16
		1977	15.2	0.037	67	0.76	0.61	0.01
	Mature	1976	14.6	0.033	16	0.41	0.54	0.03
		1977	16.8	0.036	8	0.03	0.86	0.00
F	Immature	1976	11.0	0.129	25	17.93	0.00	0.42
		1977	8.1	0.168	36	18.34	0.00	0.34
	Mature	1976	7.9	0.321	10	2.74	0.13	0.22
		1977	11.3	0.148	8	2.66	0.14	0.25
Body length (mm) with Age (days)								
M	Immature	1976	84.6	0.109	65	5.47	0.02	0.08
		1977	78.3	0.250	66	16.62	0.00	0.20
	Mature	1976	87.8	0.062	15	1.04	0.33	0.07
		1977	24.7	1.133	8	7.50	0.03	0.48
F	Immature	1976	91.4	-0.047	25	0.85	0.63	0.03
		1977	70.3	0.391	36	34.50	0.00	0.49
	Mature	1976	78.9	0.361	10	7.19	0.02	0.08
		1977	90.8	0.071	7	0.25	0.63	0.04

Note: Open groove age-class represents 17% of the sample, growth equations therefore mainly represent growth from roughly 30 to 70 days of age.

The intercept represents size at time 0 which presumably reflects size at weaning even though it has no obvious correspondence with size at birth (roughly 1.5 g and 20 mm).

Appendix 3. Correlation coefficients between gene frequency and heterozygosity at the transferrin locus, and demographic indices obtained from snap-trap catches at Heart Lake, N.W.T.

	Frequency of Fast Allele			Proportion of Heterozygotes		
	Total	OW	YG	Total	OW	YG
Current Year						
May density	-0.62	-0.70*	0.31	-0.18	-0.05	-0.36
August density	-0.71*	-0.83*	0.09	0.09	0.19	-0.02
August/May ratio	-0.21	-0.24	-0.53	0.61	0.18	0.73
Previous Year						
May density	-0.36	-0.17	-0.96**	0.14	-0.36	0.16
August density	-0.29	0.01	-0.85*	-0.01	-0.27	-0.01
August/May ratio	0.17	0.43	0.21	-0.07	0.67	-0.37

Note: Sample sizes vary between 5 and 8.

* P < 0.05

** P < 0.01

Appendix 4. Transferrin phenotypes by time periods from 1975 to 1978 in *Clethrionomys gapperi* caught in the Heart Lake area (McPhee (1977), this study).

		Overwintered						Young Immature						Young Mature					
		Male			Female			Male			Female			Male			Female		
Time	Period	FF	SF	SS	FF	SF	SS	FF	SF	SS	FF	SF	SS	FF	SF	SS	FF	SF	SS
1975	2	3	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	3	0	1	0	2	0	0	-	-	-	0	0	1	-	-	-	-	-	-
	4	1	2	5	1	3	0	1	3	0	1	0	0	1	6	2	2	3	0
	5	0	2	0	0	2	1	0	7	4	0	1	1	0	1	1	0	8	2
1976	1	0	4	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-
	2	1	12	3	1	3	1	-	-	-	-	-	-	-	-	-	-	-	-
	3	0	5	0	2	5	1	0	0	1	-	-	-	-	-	-	-	-	-
	4	1	2	2	1	10	0	0	1	1	2	2	0	2	9	5	1	8	0
	5	3	3	1	2	7	2	8	15	3	3	8	1	4	1	1	0	10	0
	6	0	1	0	0	0	0	8	18	8	6	1	4	-	-	-	1	1	0
1977	1	5	7	2	2	4	0	-	-	-	-	-	-	-	-	-	-	-	-
	2	3	4	2	4	4	1	-	-	-	-	-	-	-	-	-	-	-	-
	3	4	5	2	3	5	3	-	-	-	-	-	-	-	-	-	-	-	-
	4	4	3	3	5	5	2	4	1	0	1	1	0	0	1	1	5	4	1
	5	1	0	0	1	0	0	3	10	3	2	5	2	2	1	2	4	7	3
	6	3	6	0	1	0	0	10	16	17	6	7	6	2	6	0	2	5	3
1978	4	3	3	3	3	7	2	0	3	0	-	-	-	1	2	0	0	7	0

Note: S=Slow, F=Fast transferrin band.

Appendix 5. Calculation of relative "fitness" of transferrin phenotypes in the early-summer generation that matures in the year of its birth.

Year		FF	SF	SS	Frequency Fast	X^2
1975	Overwintered	13	24	14	0.49	
	Young mature	4	24	7	0.46	5.2*
	Expected	8.41	17.49	9.10		
	Fitness	0.48	1.37	0.77		
	Relative fitness	0.35	1.00	0.56		
1976	Overwintered	12	53	12	0.50	
	Young mature	8	29	6	0.52	5.4*
	Expected	10.75	21.50	10.75		
	Fitness	0.74	1.35	0.56		
	Relative fitness	0.55	1.00	0.41		
1977	Overwintered	37	43	15	0.62	
	Young mature	15	25	10	0.55	2.9
	Expected	18.96	23.66	7.38		
	Fitness	0.79	1.06	1.36		
	Relative fitness	0.58	0.78	1.00		
1978	Overwintered	6	10	5	0.52	
	Young mature	1	10	0	0.54	7.6*
	Expected	3.02	5.49	2.49		
	Fitness	0.33	1.82	0.00		
	Relative fitness	0.18	1.00	0.00		

Note: Expected values are calculated from the square law using overwintered gene frequencies.

X^2 test refers to fit of observed young frequencies with those expected from random mating in the parental generation.

* $P < 0.025$

Appendix 6. Calculation of relative "fitness" of transferrin phenotypes in the mid and late-summer generations that do not mature in the year of their birth.

Year		Transferrin FF	SF	SS	N†	Freq F	X²
1975	Overwintered	13	24	14	97	0.49	
	Young mature	4	24	7	117	0.46	
	Young immature	1	9	6		0.34	2.5
	Expected	3.57	7.98	4.46			
	Fitness	0.28	1.13	1.35			
	Relative fitness	0.21	0.84	1.00			
1976	Overwintered	12	53	12	210	0.50	
	Young mature	8	29	6	73	0.52	
	Young immature	23	36	13		0.57	2.3
	Expected	18.44	36.00	17.57			
	Fitness	1.25	1.00	0.74			
	Relative fitness	1.00	0.80	0.59			
1977	Overwintered	37	43	15	172	0.62	
	Young mature	15	25	10	47	0.55	
	Period 4+5						
	Young immature	8	16	5		0.55	1.0
	Expected	10.51	13.90	4.59			
	Fitness	0.76	1.15	1.09			
	Relative fitness	0.66	1.00	0.95			
	Period 6						
	Young immature	16	23	23		0.44	21.1*
	Expected	22.50	29.71	9.82			
	Fitness	0.71	0.77	2.34			
	Relative fitness	0.30	0.33	1.00			

Note: Expected values are determined from the weighted gene frequencies in both overwintered and young mature animals [e.g. parental gene frequency in 1975 is 0.475 (97•0.49+117•0.46)].

Appendix 6. (continued)

Only closed groove M^2 classes are counted in 1976 and 1977; the 1975 young immature category includes open and closed groove classes.

† Number of young born after June 19 to females caught on index traplines (used as a weighting factor to determine parental gene frequencies).

* $P < 0.001$

Appendix 7. Raw frequency of occurrence per encounter of behavioral characters (N=4825).

	Sex Category			
Variable	F vs F	M vs M	F vs M	M vs F
Nn	0.323	0.337	0.337	0.359
Neu	0.295	0.296	0.230	0.289
Str	0.178	0.205	0.142	0.137
Na	0.119	0.103	0.092	0.144
Hes	0.035	0.040	0.031	0.048
Wit	0.286	0.320	0.370	0.414
Ret	0.251	0.377	0.170	0.258
Avd	0.006	0.013	0.003	0.023
Voc	0.432	0.817	2.403	0.359
Rap	0.256	0.350	0.671	0.199
Paw	0.138	0.386	0.994	0.099
Sub	0.137	0.187	0.133	0.800
Tur	0.122	0.197	0.103	0.625
Pw1	0.074	0.151	0.673	0.071
Rai	0.054	0.119	0.122	0.051
Hud	0.138	0.111	0.163	0.162
Fol	0.040	0.096	0.071	0.159
Cha	0.027	0.116	0.035	0.035
Got	0.105	0.085	0.097	0.123
Grm	0.079	0.079	0.117	0.113
Att	0.043	0.064	0.071	0.010
Fgt	0.023	0.040	0.022	0.022
Flank scratch and digging	0.018	0.008	0.009	0.002
Perineal drag	0.006	0.003	0.004	0.006
Supine	0.002	0.004	0.004	0.000

Appendix 8. Sample sizes for neutral arena trials between wild-caught voles.

Age and Breeding Category	Year	Sex Category			
		F vs F	M vs M	F vs M	M vs F
OW vs OW	1976	94	74	23	23
	1977	82	100	20	20
Y+	1976	19	14	9	2
	1977	21	10	1	5
Y-	1976	5	16	4	5
	1977	2	18	2	2
Y+ vs OW	1976	19	14	2	9
	1977	21	10	5	1
Y+	1976	28	32	10	10
	1977	38	4	4	4
Y-	1976	10	17	8	2
	1977	25	23	13	2
Y- vs OW	1976	5	16	5	4
	1977	2	18	2	2
Y+	1976	10	17	2	8
	1977	25	23	2	13
Y-	1976	34	126	19	19
	1977	34	98	15	15

Appendix 9. Quartimax rotated solution from a Principal Components Analysis of the 22 square root transformed variables in Table 20.

	Eigenvectors							
Variable	I	II	III	IV	V	VI	VII	h^2
Nn	.89	-.05	-.04	-.03	-.04	-.07	-.03	1.0
Neu	-.24	-.08	.06	.09	-.05	.04	.79	1.0
Str	-.29	.05	.17	.07	-.10	.01	-.58	1.0
Na	.84	-.05	-.03	-.01	-.03	.01	-.06	1.0
Hes	-.08	-.05	-.06	.02	.81	.04	-.05	1.0
Wit	.50	.03	-.04	.09	.02	-.28	.38	1.0
Ret	-.19	-.05	.09	-.14	.03	.81	.03	1.0
Avo	-.05	-.03	.02	-.04	.81	.00	.04	1.0
Voc	-.02	.88	.03	-.06	-.01	.06	.01	1.0
Rap	-.03	.84	-.08	.07	-.04	-.13	-.12	1.0
Paw	-.07	.78	.05	.12	-.01	.25	-.02	1.0
Sub	.34	-.07	-.03	.70	-.01	-.07	.01	1.0
Tur	-.04	.05	.00	.87	.00	-.04	.05	1.0
Pw1	.05	.69	.00	-.17	.00	-.28	.07	1.0
Rai	-.09	.37	.32	.23	.01	.45	-.05	1.0
Hud	.80	.00	-.04	.01	-.03	-.05	-.07	1.0
Fol	.65	-.05	-.02	.16	-.03	.03	-.01	1.0
Cha	-.04	-.03	.90	.00	-.02	-.06	.05	1.0
Got	.73	-.01	-.02	.01	-.02	-.03	-.03	1.0
Grm	.50	.29	-.01	.33	.00	-.07	-.02	1.0
Att	-.08	-.01	.91	-.03	-.02	-.02	-.06	1.0
Fgt	.00	.07	.75	.00	.02	.41	.03	1.0
Eigenvalue	4.27	2.91	2.37	1.44	1.32	1.15	1.02	
% Variance	19.4	13.2	10.8	6.5	6.0	5.2	4.6	

Appendix 10. Behavioral profiles of female vs female OTUs broken down by age and reproductive categories (Mean, SE).

ID	Category	Factor						
		AMI	THR	AGG	SBT	AVD	BOX	APV
1	OW vs OW	-0.26	-0.02	-0.02	-0.01	-0.02	-0.01	-0.02
		0.04	0.05	0.06	0.04	0.05	0.06	0.05
2	Y+	-0.27	-0.11	0.30	-0.22	-0.11	-0.31	-0.16
		0.08	0.09	0.17	0.03	0.06	0.09	0.09
3	Y-	-0.02	0.10	0.51	0.78	-0.22	-0.61	-0.29
		0.45	0.20	0.57	0.75	0.05	0.29	0.26
4	Y+ vs OW	-0.08	-0.33	-0.18	-0.09	0.07	0.23	0.18
		0.12	0.05	0.03	0.09	0.10	0.09	0.10
5	Y+	-0.24	-0.04	0.06	-0.02	-0.01	0.17	-0.05
		0.08	0.08	0.08	0.09	0.06	0.12	0.07
6	Y-	0.07	-0.17	0.01	-0.20	-0.16	-0.13	-0.03
		0.14	0.11	0.14	0.05	0.03	0.05	0.11
7	Y- vs OW	0.93	0.63	-0.18	-0.50	-0.16	0.40	0.48
		1.11	0.85	0.07	0.27	0.04	0.42	0.52
8	Y+	0.20	-0.07	-0.21	-0.24	-0.07	0.14	0.17
		0.16	0.13	0.02	0.13	0.04	0.11	0.10
9	Y-	0.46	-0.28	-0.20	-0.14	0.02	-0.04	-0.03
		0.17	0.06	0.01	0.07	0.09	0.04	0.08

Appendix 11. Behavioral profiles of male vs female OTUs broken down by age and reproductive categories (Mean, SE).

ID	Category	Factor						
		AMI	THR	AGG	SBT	AVD	BOX	APV
19	OW vs OW	0.25	-0.29	-0.08	1.48	0.56	-0.04	0.18
		0.12	0.08	0.06	0.37	0.29	0.08	0.09
20	Y+	-0.19	-0.36	0.00	1.51	-0.04	0.53	0.69
		0.18	0.13	0.16	0.75	0.12	0.60	0.36
21	Y-	0.08	-0.42	0.08	-0.04	-0.21	-0.18	0.18
		0.26	0.07	0.22	0.15	0.03	0.11	0.29
22	Y+ vs OW	-0.22	0.02	-0.09	0.26	0.20	0.32	0.19
		0.11	0.22	0.08	0.28	0.19	0.44	0.17
23	Y+	-0.30	-0.23	-0.16	0.54	0.03	-0.02	0.06
		0.13	0.14	0.11	0.47	0.15	0.13	0.20
24	Y-	0.28	-0.28	-0.22	0.09	-0.18	-0.21	-0.19
		0.37	0.18	0.05	0.10	0.03	0.10	0.12
25	Y- vs OW	-0.13	0.07	-0.23	-0.08	-0.07	0.21	-0.10
		0.34	0.29	0.06	0.18	0.13	0.37	0.30
26	Y+	0.38	-0.10	-0.19	-0.19	-0.02	-0.08	0.18
		0.23	0.16	0.02	0.13	0.16	0.10	0.16
27	Y-	0.57	-0.13	-0.18	-0.13	-0.17	-0.12	-0.09
		0.16	0.11	0.02	0.07	0.01	0.06	0.09

Appendix 12. Behavioral profiles of female vs male OTUs broken down by age and reproductive categories (Mean, SE).

ID	Category	AMI	THR	AGG	SBT	AVD	BOX	APV
		Factor						
28	OW vs OW	-0.19	1.72	-0.04	-0.24	-0.11	-0.02	-0.05
		0.07	0.40	0.08	0.05	0.04	0.20	0.12
29	Y+	-0.42	-0.01	1.28	0.07	-0.23	-0.70	-0.18
		0.09	0.18	0.58	0.29	0.42	0.32	0.35
30	Y-	-0.24	-0.19	0.13	0.13	0.17	-0.14	0.47
		0.09	0.22	0.38	0.24	0.37	0.15	0.43
31	Y+ vs OW	-0.47	1.09	0.69	-0.32	0.24	0.03	-0.40
		0.06	0.56	0.73	0.13	0.46	0.23	0.25
32	Y+	-0.34	0.22	0.25	-0.10	0.18	-0.38	-0.15
		0.12	0.25	0.27	0.11	0.25	0.15	0.19
33	Y-	0.35	-0.27	-0.04	-0.01	-0.11	-0.14	-0.32
		0.27	0.09	0.12	0.13	0.06	0.10	0.12
34	Y- vs OW	-0.07	-0.11	-0.23	-0.24	-0.09	-0.02	-0.25
		0.25	0.17	0.04	0.05	0.09	0.15	0.10
35	Y+	0.49	-0.14	-0.16	-0.23	0.07	-0.17	0.34
		0.61	0.15	0.05	0.10	0.24	0.14	0.27
36	Y-	0.52	-0.23	-0.17	-0.06	-0.12	-0.19	0.06
		0.17	0.08	0.02	0.13	0.04	0.06	0.09

Appendix 13. Behavioral profiles of male vs male OTUs broken down by age and reproductive categories (Mean, SE).

ID	Category	Factor						
		AMI	THR	AGG	SBT	AVD	BOX	APV
10	OW vs OW	-0.36	0.06	0.39	0.03	0.20	0.21	-0.16
		0.05	0.07	0.17	0.07	0.09	0.10	0.05
11	Y+	-0.24	0.04	0.28	-0.08	-0.19	-0.16	-0.08
		0.12	0.20	0.22	0.09	0.04	0.16	0.15
12	Y-	-0.10	-0.23	0.02	0.38	-0.22	-0.04	-0.15
		0.14	0.16	0.14	0.31	0.02	0.10	0.15
13	Y+ vs OW	-0.32	-0.04	-0.05	-0.07	-0.11	0.24	-0.23
		0.10	0.12	0.14	0.12	0.12	0.10	0.11
14	Y+	-0.42	0.13	-0.12	-0.08	0.16	0.03	0.00
		0.05	0.19	0.07	0.10	0.12	0.13	0.10
15	Y-	-0.08	-0.12	-0.13	0.02	-0.04	-0.16	0.07
		0.11	0.12	0.06	0.13	0.09	0.06	0.10
16	Y- vs OW	-0.14	0.75	-0.21	-0.29	0.07	0.21	0.03
		0.13	0.32	0.03	0.06	0.11	0.10	0.10
17	Y+	-0.12	0.10	-0.13	-0.18	0.11	-0.15	0.13
		0.10	0.13	0.06	0.06	0.22	0.07	0.09
18	Y-	0.62	-0.09	-0.16	-0.09	-0.07	-0.13	0.02
		0.10	0.04	0.01	0.04	0.02	0.03	0.04

Appendix 14. Multiple regression analyses of factor scores with miscellaneous variables.

Variable	Factor							
	AMI	THR	AGG	SBT	AVD	BOX	APV	D†
1. OW F vs OW F (N=141)								
Year	+	NS	NS	NS	NS	NS	NS	NS
Molar root length	NS	NS	NS	NS	NS	NS	+	NS
Corrected weight	NS	NS	+	NS	NS	+	NS	NS
Body length	NS	NS	NS	NS	NS	-	-	NS
Rank of capture	NS	NS	NS	NS	NS	-	NS	NS
Days from capture to trial	NS	NS	NS	NS	NS	+	NS	NS
Variables in model	1		1			4	2	
Significance	0.01		0.00			0.00	0.01	
Multiple r^2	0.04		0.08			0.20	0.07	
2. OW M vs OW M (N=150)								
Year	NS	+	NS	NS	NS	NS	NS	NS
Day of trial	+	NS	NS	NS	NS	NS	NS	NS
Rank of capture	NS	NS	-	NS	NS	+	NS	NS
Days from capture to trial	NS	+	NS	NS	NS	NS	NS	NS
Variables in model	1	2	1			1		
Significance	0.03	0.00	0.02			0.03		
Multiple r^2	0.03	0.07	0.04			0.03		

(Continued)

Appendix 14. (continued)

Variable	AMI	THR	AGG	SBT	AVD	BOX	APV	D†
3. Y- M vs Y- M (N=156)								
Year	-	NS	-	NS	NS	NS	NS	NS
Day of trial	+	NS	NS	NS	NS	-	NS	NS
Familiarity	NS	NS	NS	NS	NS	+	NS	NS
Days from capture to trial	NS	-	NS	-	NS	+	NS	NS
Variables in model	2	1	1	1		3		
Significance	0.00	0.00	0.00	0.01		0.00		
Multiple r²	0.10	0.07	0.06	0.04		0.15		

Note: Familiarity refers to whether or not the animal and its opponent were caught on the same trapline, rank of capture refers to when the animal was caught on the trapline (1st, 2nd, etc. trap check).

+: positive slope, -: negative slope,
NS: not significant

† Dominance Index